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VOLUME 37

SYSTEMATIC PLANT STUDIES

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Director, United States National Museum.

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***Errata: Line 22, page 425, should read "Stemonitis hyperopta . . ."**

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STUDIES OF PACIFIC ISLAND PLANTS, XVII

THE GENUS GENIOSTOMA (LOGANIACEAE) IN THE NEW HEBRIDES, FIJI, SAMOA, AND TONGA

By ALBERT C. SMITH and
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STUDIES OF PACIFIC ISLAND PLANTS, XVII [1]

THE GENUS GENIOSTOMA (LOGANIACEAE) IN THE NEW HEBRIDES, FIJI, SAMOA, AND TONGA

ALBERT C. SMITH AND BENJAMIN C. STONE

Introduction

Specimens of *Geniostoma*, an essentially tropical Old World genus of woody flowering plants of the family Loganiaceae, have been accumulating in world herbaria, including that of the U.S. National Museum, over a period of several decades, during which no serious attempt to understand relationships within the genus has been made. Specific identifications have usually proved difficult, and the genus as a whole is in need of a complete systematic revision. Primarily in order to facilitate an understanding of the Fijian specimens, which are now reasonably abundant in herbaria, we have undertaken a regional revision within a small portion of the generic range, extending from the New Hebrides eastward to Samoa. It has been customary to throw together a large part of the Pacific *Geniostomata* under the name *G. rupestre* J. R. & G. Forst., in spite of the fact that Gilg & Benedict (in Bot. Jahrb. 56: 542. 1921) considered it a local endemic of the New Hebrides. Only in New Caledonia, Samoa, and to a lesser extent in Micronesia have studies of *Geniostoma* progressed to a point where identifications can be made with any degree of assurance. For the Malaysian region in the broad sense there exist no dependable treatments, a situation that one may hope to see corrected as work on the Flora Malesiana progresses.

As is so often the case in "difficult" genera, the older descriptions are mostly inadequate for an understanding of the identity of species. Fortunately we have been able to see types or isotypes of most taxa thought to occur in our region. Especially valuable for study has been type material of *G. rupestre*, the type species of the genus. *Geniostoma* has in general been correctly understood and delimited,

[1] This paper, based on research partially supported by a grant from the National Science Foundation, continues the series under the same title by the first author. The place of publication of nos. X–XIV in the series was noted in connection with no. XV, in Contr. U.S. Nat. Herb. 30: 523–575. 1953. No. XVI was published in Journ. Arnold Arb. 34: 97–124. 1953.

but we believe that concepts of some of its species have been unreasonably broad. Sixteen species are now believed to occur between the New Hebrides and Samoa, of which six are here described as new. The other species of our region are redescribed on the basis of available material and older descriptions, and we append notes on distributions, local names, and relationships.

In the course of this study the pertinent herbarium material of several institutions has been examined and is here cited, with the indicated abbreviations: Arnold Arboretum of Harvard University (A); Bernice P. Bishop Museum (Bish); British Museum (BM); Gray Herbarium of Harvard University (GH); Royal Botanic Gardens, Kew (K); New York Botanical Garden (NY); University of California at Berkeley (UC); and U.S. National Herbarium (US). We are indebted to the administrators of these herbaria for the opportunity of studying specimens under their care.

HISTORICAL SKETCH

The genus was described by J. R. & G. Forster in their "Characteres Generum," in 1776, as was also their type species, *G. rupestre*, and was based upon material obtained by them on the island of Tanna, in the New Hebrides, during Cook's second voyage. The generic name is formed from the Greek words *genias* (beard) and *stoma* (mouth) and of course should be treated as neuter (cf. Int. Code Bot. Nomencl. Rec. 75A. 1956); when necessary we have corrected epithets given a feminine form. Additional species of *Geniostoma* were described in the early part of the nineteenth century from the Mascarene Islands, Java, Sumatra, the Philippines, New Zealand, Australia, and the Marianas Islands. For the most part, however, specimens obtained in Polynesia and Melanesia were identified with *G. rupestre*. In 1880 H. Baillon (in Bull. Soc. Linn. Paris 1: 247–248) published a list of New Caledonian species of the genus. Various other species described in *Geniostoma*, including those from the New World, were later shown to belong to other genera; the Hawaiian species, for instance, have been removed to the closely related genus *Labordia* Gaud. The first treatment of the genus that was relatively broad in regard to geography and in addition was acute and analytical was that of T. Valeton (in Bull. Inst. Bot. Buitenz. 12: 1–28. 1902), who studied the species of the vicinity of Buitenzorg and also some of those from more distant regions. Although he did not attempt a monographic revision, he employed a number of new criteria in his specific distinctions and was apparently the first to recognize the sexual dimorphism of several of the species. During the present century the number of putative species has substantially increased and now approaches 100, but the arrangement of the species within the genus has been neg-

lected. There almost certainly remain undescribed species in New Guinea and the other large islands of Malaysia and Melanesia. In Micronesia, and in the Society Islands and Polynesia generally, most or all of the species may have been discovered. According to A. Guillaumin (Fl. Anal. Syn. Nouv.-Caléd. 285. 1948), none of the New Caledonian species occur outside that area except for *G. rupestre*. As in other genera, the islands between Fiji and New Guinea have disclosed fewer *Geniostomata* than might be anticipated, indicating the need of further field work there.

CRITERIA OF USE IN SPECIFIC DELIMITATION

Among vegetative features of *Geniostoma*, the unusual nature of the stipules of two Fijian species, *G. macrophyllum* and *G. stipulare*, deserves mention. In these species the stipules are large, adnate to the margins of the petioles and forming foliaceous sheaths that are soon disrupted, leaving traces of tissue or obvious linear scars on the petiole. Both of these species are further distinguished by several other significant characters; they have cauline or ramuline inflorescences and leaves large for the genus. Their relationship may possibly be with *G. caulocarpum* K. Schum., of New Guinea. With the exception of *G. macrophyllum* and *G. stipulare*, the species treated by us have intrapetiolar stipules of a type more characteristic of the genus, forming a short sheath scarcely exceeding 2 mm. in length.

Certain species of our region are characterized by having markedly quadrangular or even 4-winged branchlets; the Samoan *G. fleischmannii* has the branchlets narrowly alate, as do some species of New Caledonia. *Geniostoma insulare* has its branchlets at least in the ultimate internodes sharply quadrangular. However, most of our species have essentially terete branchlets, which in the juvenile internodes may be compressed or subquadrangular.

Other vegetative characters of potential taxonomic usefulness include the kind and degree of pubescence and the size and shape of leaf-blades. Pubescence of the vegetative parts in general is limited to the innovations, although in certain species it is persistent; in the Fijian *G. calcicola*, for instance, a short, dense indument covers both surfaces of the leaf-blades, a character noted otherwise among species of the vicinity only in *G. crassifolium* Benth., of the Isle of Pines. Leaf-size and shape are characters at best of secondary importance. The leaf-blades may be fairly consistently large (in *G. macrophyllum* and *G. stipulare*) or small (in *G. stenocarpum*), but in most species-complexes the range of size is too great to be of taxonomic value. In leaf-shape there is a somewhat wider array of types and perhaps a slightly greater taxonomic value, but, as Valeton cautioned in 1902,

leaf-shape alone is not dependable in *Geniostoma* and must be used in conjunction with other characters.

One species of our area, the Samoan *G. biseriale*, has essentially sessile leaves that at once distinguish it from others of the region. Other species with similarly subsessile leaves are *G. sessile* Kanehira (Palau), *G. rapense* F. Br. (Rapa), and *G. clavatum* J. W. Moore (Raiatea), but they are diverse in other respects and obviously do not form a natural species group.

The basic structural unit of the inflorescence is a dichasium, generally of the cymose type; this is much modified, and finds its extreme diversity in the multiflowered, glomerate, cauline inflorescences of *G. macrophyllum*, which may bear up to 200 flowers, these basically organized in congested triflorous dichasia. At the other extreme may be mentioned the highly reduced, simple cyme of *G. calcicola*, with its 5 flowers on moderately long pedicels. In some New Caledonian species the inflorescence is reduced to a single flower. The most common type of inflorescence in the genus is a moderately open, compound dichasium with perhaps 5 to 30 flowers, those of the distal axes generally in triflorous dichasia, but those lower on any inflorescence-branchlet sometimes irregular, single, or paired. The inflorescences in leaf-axils (characteristic of most species) may consist of a single cyme but frequently are fasciculate (usually at the first node of the peduncle but sometimes in the axil itself) in pairs or sometimes in threes. In discussing the inflorescence of *Geniostoma*, Valeton discerns a racemose and a paniculate type, which he terms bostryx and cyme. According to Rickett (in Bull. Torrey Bot. Club 82: 430. 1955), these are but modifications of the dichasium. The verticillaster described by Valeton seems also a modification of the dichasium, with an obsolete or absent peduncle and fasciculate rachises. Corymbose panicles, according to Valeton present in *G. avene* Valeton and *G. australianum* F. v. Muell., are also basically dichasial. The main rachis is branched into opposite laterals, which are subtended by bracts, each node thus being bibracteate; on the irregular (not triflorous) branchlets there may be single unpaired bracts, or a pair of bracts without branchlets in their axils. In most inflorescences the calyces are subtended by bracteoles. In general, the nature of the inflorescence is diagnostic for only a few unusual species (e.g. in our area *G. gracile*, *G. macrophyllum*, *G. insulare*, and perhaps *G. calcicola*), but still it provides a valuable supplementary character in delimiting taxa.

The pioneering work of Valeton in *Geniostoma* has elucidated the incipient and actual sexual dimorphism in various species and has explained the diverse types of gynoecia. Dimorphism is expressed in some species by a considerable difference in stylar length, and in addition by the form and pubescence of the stamens. In general,

it would appear that flowers with long styles are those with fertile anthers, while those having short styles have sterile anthers. In the species of our area, however, marked dimorphism is not obvious, and short-styled flowers frequently appear to have fertile anthers. The close approach to dioecism that Valeton discussed in relation to certain Javanese species is lacking in the Fijian-Samoan area, at least as far as can be ascertained from gross microscopic observations. However, in certain cases, e.g. in *G. vitiense*, there is a fairly marked heterostyly, accompanied by anther differences. Stylar length is thus seen to be a character related to sexual dimorphism, and as such it is hardly appropriate for use in specific distinctions. In this regard, one may wonder whether the species from Saipan described as *G. longistylum* by Gilg is merely a long-styled form of *G. micranthum* DC. or *G. hoeferi* Gilg & Benedict; students of Micronesian species should review *Geniostoma* with this in mind.

The presence or absence of trichomes on the anthers, found to be of some use in the species discussed by Valeton, is apparently of little or no consequence in our species. The shriveled thecae of the sterile anthers mentioned by Valeton are not obvious in specimens from our region; at least we have noted no anthers that appear to be sterile, although of course it is possible that non-fertile pollen or reduced fertility exist in some cases. In respect to floral dioecism in the species of our area, there seems to be little or no sterilization of the gynoecia. Incipient tendencies seem to be toward hermaphrodite vs. pistillate individuals, but these tendencies are of no present taxonomic use.

Significant specific differences are found in the venation of the corolla, although these differences are difficult to express verbally without resorting to lengthy and complex phrases. We have included an illustration for each species here treated (Plate 1) showing the corolla split between two lobes and flattened out (two lobes are omitted from each sketch for brevity). In one basic type of corolla-venation, illustrated by *G. confertiflorum*, *G. clavigerum*, and *G. uninervium*, each corolla-lobe is supplied by a single main nerve, which may produce a few lateral branches, but these are so few or so inconspicuous that the impression of a one-nerved lobe is given. A second type of venation is more complex and could be described as somewhat candelabriform. In this type the main central nerve supplying each lobe has one or more laterally produced pairs of branches, these either subparallel or arcuately ascending and in turn usually laterally branched. Among our species the nerves anastomose and form reticulations only in *G. dictyoneurum*, in other species being free in the lobes. Whether the main vein supplying each lobe sends out its first branches high or low in the corolla provides a character of some

use. A division into three veins at or near the base of the corolla-tube frequently occurs in such species as *G. rupestre* and *G. macgregorii;* elsewhere, as in *G. stenocarpum* and *G. insulare*, the main vein usually branches first near the summit of the corolla-tube or in its throat. However, there is no real consistency within species as to this venation-pattern, and it should be used with caution as a differentiating character, even though incipient trends are apparent. For the most part the venation is readily observed in corollas of relatively thin texture; in species with a more carnose corolla that organ must be boiled and the outer tissue separated with dissecting tools, the venation then being apparent. The venation of the calyx, which usually has three nerves ascending into each lobe, provides a less useful character in species differentiation.

In most species of *Geniostoma* in our area the corolla is glabrous without, but all species observed by us have an obvious indument in the throat. The trichomes of the corolla-throat are white, thin, and retrorse, but as they sometimes extend to the inner surface of the lobes they tend to become spreading or even ascending. The length of the corolla-throat trichomes provides a very useful and consistent character. Among our species these trichomes are either "short" (0.1–0.4 mm. long) or "long" (0.4–0.9 mm. long); while such a dimensional difference is not striking, there appear to be no species in which a decision is difficult. Of course detection and measurement of so minute a character are facilitated by adequate microscopic and micrometric equipment, but even with a hand lens one can usually decide whether the trichomes are "short" or "long."

Pubescence similar to that within the corolla-throat extends to the filaments; rarely the anthers also bear trichomes of the same type. The gynoecium in *Geniostoma* is characteristically glabrous, but one of our species, *G. macrophyllum*, differs strikingly in having its ovary copiously hirtellous on the distal surface. The style only rarely is weakly hirtellous. The stigmas form a globose or clavate to obovoid capitulum that is minutely papillate, with papillae essentially conical but sometimes so slender as to appear setulose. It may be added here that the radial nature of the stigma, with the papillae in marked radial groups as shown in the Forsters' plate (*t. 12*), has been noted in *G. vitiense*.

A marked and diagnostic character found in certain Malaysian species, that of mucronulate or apiculate anthers, is of less importance in our area. However, in some instances (e. g. in *G. samoense* var. *parviflorum*) there does appear to be a very minute mucro on the anther. There is also some indication that apiculation of the anthers may be correlated with incipient sexual dimorphism, as mentioned and illustrated under *G. vitiense* and *G. macgregorii.* However,

all of our species fundamentally have obtuse or merely acute anthers, unlike such species as *G. arboreum* (Bl.) Kuntze (=*G. haemospermum* Steudel) and *G. miquelianum* Koorders & Valeton as described by Valeton.

The capsules in our species are usually ellipsoid to ovoid or obovoid, briefly apiculate by the persistent base of the style. However, a tendency toward essentially globose capsules is seen in *G. insulare* f. *sphaerococcum* and *G. dictyoneurum*. The capsules are subtended by persistent calyces, and all of them dehisce into two recurved valves to expose the seminal mass. The degree of recurvature of the valves, mentioned by Valeton, seems to us of little or no diagnostic use.

In summarizing this discussion of specific criteria, we agree with earlier students of *Geniostoma* in finding none of them entirely satisfactory. In approximate order of usefulness in differentiating the species of our region may be mentioned: type of stipule, presence or absence of ovary-indument, length of trichomes of the corolla-throat, type and abundance of vegetative pubescence, position and type of inflorescence and number of flowers, corolla-venation, stigma-shape, capsule-shape, and terete vs. angled or winged branchets. Various combinations of these characters and others of lesser value permit the recognition of taxa that seem to possess stability. That our delimitation of taxa is somewhat subjective is obvious, but this is inevitable in a study where experimental methods are impracticable.

Systematic Treatment

Geniostoma J. R. & G. Forst. Char. Gen. 24. *t. 12*. 1776.

As presently known, *Geniostoma* is composed of about 95 species of trees and shrubs. It is exclusively Old World in distribution, occurring from the Mascarene Islands through Malaysia north to Kyushu (Japan) and the Marianas and East Caroline Islands, south to Australia and New Zealand, and east to the Society Islands. The species at the extreme north and south limits of the genus are *G. ligustrifolium* A. Cunn. (New Zealand), *G. petiolosum* C. Moore & F. v. Muell. (Lord Howe Island), and *G. glabrum* Matsumura (Japan). Many species are ecologically correlated with the coastal lowland vegetation of tropical islands, but increasing numbers are becoming known from the cool, wet forests of the high interiors of such large islands as New Guinea.

Characteristic features of the genus are the presence of stipules, the simple opposite leaves, the axillary or cauline dichasial inflorescences, the tubular 5-lobed calyx and corolla, the insertion of the 5 stamens on the corolla-tube near its throat, the bilocular ovary, the numerous anatropous or nearly amphitropous ovules, and the bivalved, capsular,

dehiscent fruits with seeds embedded in an eventually exposed pulpy mass. The persistence of the seed-mass between the valves of the dehisced capsule is noteworthy; the seeds remain on persistent funicles and are enclosed by the pulp, which dries to a thin pellicle; the placentation persists until at last the mass drops or is broken from the exocarp and then splits into two halves, corresponding to the contents of each locule of the ovary. The seeds are ovate-angulate, usually concave at the hilum and minutely papillate; the embryo, embedded in a small amount of smooth endosperm, is short-oblong, usually more than half the length of the seed, and very shortly divided at apex into two cotyledons.

Key to the Species

Stipules large, forming foliaceous sheaths 1–3.5 cm. long, adnate to margins of petioles and caducous, leaving obvious linear scars; leaves large for the genus, the blades often exceeding 30×15 cm. (but sometimes smaller); inflorescences borne on trunks or branches or defoliate branchlets; Fijian species.

Ovary copiously hirtellous on distal surface; corolla-lobes glabrous (except at base within); inflorescences cauline, glomerate to elongate (to 25 cm. long) and with as many as 200 flowers; leaves glabrous . . **1. G. macrophyllum**

Ovary glabrous; corolla-lobes densely hirtellous within; inflorescences ramuline, dichasial, 15–20-flowered; leaf-blades (as well as other young parts) copiously pubescent beneath at least on principal nerves, the trichomes predominantly 3-celled, about 0.5 mm. long . . . . . **2. G. stipulare**

Stipules intrapetiolar, small, forming inconspicuous sheaths no more than 2 mm. long, the petioles without obvious stipular scars; leaves comparatively small, the blades not exceeding 24×13 cm. and usually much smaller; inflorescences axillary or rarely on defoliate branchlets.

Leaves obviously petiolate, the petioles normally at least 4 mm. long, the blades various at base (acute or attenuate to rounded) but not cordate.

Corolla-venation comparatively simple, each lobe supplied by a single nerve with a few short faint laterals, or essentially unbranched; trichomes of the corolla-throat obvious, 0.6–0.7 mm. long; Fijian species.

Stigma oblong-clavate, obovoid, or ellipsoid; each corolla-lobe supplied by a faint nerve with 1 or 2 usually unbranched laterals on each side.

Leaves comparatively large, the petioles 9–20 mm. long, the blades usually 10–23×5–12 cm.; inflorescences 5–11-flowered; corolla-lobes with a single pair of faint lateral nerves arising from the midnerve . . . . . **3. G. confertiflorum**

Leaves smaller, the petioles 5–9 mm. long, the blades 3–8×1–3.6 cm.; inflorescences 3–5 (rarely to 9)-flowered; corolla-lobes with 2 pairs of lateral nerves arising from the midnerve . . **4. G. clavigerum**

Stigma globose; each corolla-lobe supplied by a single dark relatively conspicuous nerve with brief and obscure (or usually without) laterals; petioles 5–9 mm. long, the leaf-blades ovate, usually about 10–12×3–5 cm . . . . . **5. G. uninervium**

Corolla-venation comparatively complex, each lobe supplied by a nerve that produces in the corolla-tube (or at its base) one or several pairs of obvious lateral nerves, these ascending together into the lobe and usually rebranched.

Trichomes of the corolla-throat short, 0.1–0.4 mm. long.
Indument of young parts of plant copious, although minute, composed of setulose trichomes 0.05–0.2 mm. long, these obvious on the young branchlets, petioles, and often on ventral surfaces of leaf-blades, especially on costae; inflorescence-branches similarly pilose; Fiji to Tonga and Niue . . . . . **6. G. vitiense**
Indument lacking throughout (except within corolla).
Inflorescences elongate, with branchlets and pedicels 7–17 mm. long, 3–7-flowered; corolla-lobes glabrous and smooth, each supplied by a nerve that branches high in the tube or in the throat; stigma clavate-obovoid; capsules ellipsoid, 5–9×4–7 mm.; Samoa. **7. G. gracile**
Inflorescences comparatively compact, with branchlets and pedicels 2–6 mm. long, 5–15(–20)-flowered; corolla-lobes pilose proximally or pustulose within, each supplied by nerves diverging in lower part of tube or at its base; stigma globose; capsules narrower, 7–13×3–4.5 mm.; Fiji and Tonga . . . . . **8. G. macgregorii**
Trichomes of the corolla-throat comparatively long, 0.4–0.9 mm. long.
Leaf-blades puberulent on both surfaces (hairs obvious, about 0.3 mm. long), elliptic, 3.5–5×1.5–2.5 cm., rounded at apex; Fiji. **9. G. calcicola**
Leaf-blades glabrous, or pilose only on the ventral costae, variously shaped but most often acute to acuminate at apex.
Corolla-venation complex, each lobe supplied by a nerve branched in lower portion of tube, the branches rising into the lobe and there forming a reticulum of short veinlets; leaf-blades thin in texture, ovate, 7–12×3.5–7 cm., usually rounded at base and apex; Fiji . . . . . **10. G. dictyoneurum**
Corolla-venation not reticulate, the veinlets in the lobes free.
Flowers comparatively large, the corolla 4.5–5 mm. long, each lobe supplied by a dichotomous main nerve with several laterals; leaf-blades oblanceolate or narrowly elliptic, 4–12×1.5–3.5 cm.; branchlets quadrangular and narrowly winged distally; Samoa . . . . . **11. G. fleischmannii**
Flowers comparatively small, the corolla 2.5–3.5 mm. long, each lobe supplied by a single main nerve with 1 or 2 pairs of laterals; branchlets not winged.
Leaf-blades lanceolate or narrowly ovate, 4–7.5×1.2–2.7 cm.; each corolla-lobe supplied by a nerve divided in the throat; Fiji . . . . . **12. G. stenocarpum**
Leaf-blades various in shape, usually exceeding 8×3 cm.
Inflorescence-axes minutely puberulent with trichomes no more than 0.03 mm. long; vegetative parts glabrous; leaf-blades ovate to broadly ovate, 8–18×4–9 cm. (often smaller in var. *parviflorum*); Samoa . . **13. G. samoense**
Inflorescence-axes glabrous (or, if puberulent in some forms of no. 15, then the young vegetative parts also puberulent).
Leaf-blades acuminate or obviously cuspidate at apex; each corolla-lobe supplied by a nerve usually branching at or near base of tube; New Hebrides and Santa Cruz Islands, and perhaps westward . . . . **14. G. rupestre**

Leaf-blades rounded to obtuse (or sometimes broadly acute or bluntly cuspidate) at apex; each corolla-lobe supplied by a nerve usually branching in upper part of tube; Fiji to Samoa, Tonga, and Niue . . . . . **15. G. insulare**

Leaves subsessile, the petioles 2 mm. long or less, the blades subauriculate, cordate, or subcordate at base; plant glabrous throughout except for the usual corolla-throat trichomes, these 0.3–0.4 mm. long; Samoa.

16. G. biseriale

1. Geniostoma macrophyllum Gillespie in Bishop Mus. Bull. 91: 25, *fig. 28*. 1932.

PLATE 1, FIGURE 1; PLATE 2, FIGURES 1–3

Small tree to 10 m. high, glabrous throughout except for some floral parts, the trunk to 25 cm. in diameter; branchlets stout, distally 4–8 mm. in diameter and compressed-quadrangular, becoming terete and up to 2 cm. in diameter; stipules forming a foliaceous sheath up to 15 mm. long, distally acute, laterally united with the alate petiole-margin; leaves large for the genus, the petioles broadly alate, not distinct from the blade, the blades chartaceous, ovate to elliptic or sometimes obovate, 22–55 cm. long, 9–25 cm. broad, gradually decurrent at base and produced laterally along the petiole into a broad decurrent wing, obtuse to bluntly cuspidate at apex, entire at margin, the costa stout, conspicuous, sulcate above, prominently elevated beneath, the secondary nerves 11–20 pairs, arcuate-ascending, irregularly anastomosing near margin, slightly sulcate above, raised beneath, the veinlets prominulent on both surfaces; inflorescences cauline on old wood, often near base of trunk, variable in size and shape, when young somewhat glomerate, at length more or less pendent on elongated branching woody axes bearing numerous congested triflorous dichasia, sometimes up to 25 cm. long and bearing as many as 200 flowers, freely branching, with deltoid, acute, inconspicuous bracts and small ultimate bracteoles less than 1 mm. long; flowers subsessile in congested groups of 3; calyx cupuliform, about 2 mm. in diameter, lobed to the middle, the lobes deltoid-ovate, acute, 1–3 (–5)-nerved, the nerves free; corolla 3–3.3 mm. long, divided to middle, the tube 1.5–1.7 mm. long, pilose at throat, the trichomes about 0.6 mm. long, dispersed in a uniform band around throat down to middle of tube, the lobes deltoid-ovate, about 1.5× 1.5 mm., glabrous without and within except at extreme base at throat, the venation comparatively simple, each corolla-lobe supplied by a single usually 3-branched vein, the branches arising midway in the tube; stamens with short glabrous or sparsely ventrally barbate filaments about 0.3 mm. long, the anthers broadly ovoid, about 0.5 mm. long, sparsely hirtellous at base, acute at apex; ovary depressed-globose, conspicuously flattened distally, about 0.6 mm. high and 1.6 mm. in diameter, laterally glabrous but copiously hirtellous on distal surface with erect hairs about 0.2 mm. long, the style gla-

brous, 0.4–0.5 mm. long, the stigma depressed-globose, papillate, about 0.5 mm. broad; capsules glabrous, ovoid-ellipsoid, apiculate by the stylar remnant, 8–11 mm. long.

TYPE LOCALITY: Near Nasinu, Naitasiri Province, Viti Levu, Fiji; the type is *Gillespie* 3638, cited below.

DISTRIBUTION: Endemic to Fiji, and known thus far only from Viti Levu, Vanua Levu, and Ovalau, as a slender tree 3–10 m. high, with a trunk 4–10 (–25) cm. in diameter, occurring in wet forests at altitudes from near sea level to 850 m. The inflorescences, which consist of dense many-flowered glomerate or elongate irregular dichasia, are borne on the trunk, often less than a meter from the ground. The corolla is noted as greenish white, within hirtellous with whitish hairs; other floral parts are whitish. The capsule at maturity is black, with orange seeds. No local names or uses are indicated.

FIJI: VITI LEVU: Mba: Hills between Nandala and Nukunuku Creeks, along trail from Nandarivatu toward Lewa, *Smith* 6168 (A, Bish, K, US). Serua: Hills along coastal road, *Greenwood* 976A (A). Namosi: Hills east of Wainikoroiluva River near Namuamua, *Smith* 8899 (US); hills bordering Wainavindrau Creek, near Wainimakutu, *Smith* 8552 (US); hills east of Navua River, *Greenwood* 976 (A). Naitasiri: Near Viria, *Parks* 20461 (Bish, UC); along Tamavua-Sawani road, *Setchell & Parks* 15071 (Bish); near Nasinu, *Gillespie* 3638 (Bish type, GH, UC); near Suva Pumping Station, *Degener & Ordonez* 13746 (A, Bish, K, NY). Naitasiri or Rewa (near border): Mt. Kombalevu, *Parks* 20317 (Bish, UC, US); near Tamavua, *Jeoward* 65 (K); woods near Tamavua, *Gillespie* 2109 (Bish). Rewa: Slopes of Mt. Korombamba, *Gillespie* 2297 (Bish); Suva Ditch Trail, *Bryan* 370 (A, Bish); Princes Road, *Meebold* 16791 (Bish); Central Road, Suva, *Tothill* 613 (Bish, K), 617 (K). VITI LEVU, without locality, *Parks* 20870 (Bish, UC). VANUA LEVU: Thakaundrove: Southern slope of Korotini Range, below Navitho Pass, *Smith* 573 (Bish, GH, K, NY, UC, US). OVALAU: Near summit of main range west of Levuka, *Gillespie* 4449 (Bish, UC); Mt. Tana Lailai, near Levuka, *Graeffe* in 1864 (K).

Geniostoma macrophyllum, together with the new species *G. stipulare*, is isolated in relation to the other species of our area in gross and obvious features as well as in technical characters. These two species exhibit certain vegetative characteristics in common: unusually large leaves; enlarged, petiolar stipules; and cauliflory or ramuliflory. In particular, the nature of the stipules, which in both species are adnate to the margins of the petiole and in *G. macrophyllum* united to the basal part of the blade also, marks these species as amply distinct from their Fijiian congeners, and indeed from most of the other Pacific species which have been the subject of our attention.

Geniostoma macrophyllum is abruptly distinct from *G. stipulare*, and displays very little intraspecific variation of consequence. Only one specimen (*Jeoward* 65) is unusual, in that its leaves are markedly obovate and more or less cuspidate at apex, and in addition, the branches of the inflorescence are excessively elongated; yet the

flowers are indistinguishable from those of the other cited specimens of *G. macrophyllum*.

The phenomenon of cauliflory is more marked in *G. macrophyllum* than in other species of the genus, with the exception of *G. caulocarpum* K. Schum., of New Guinea, the inflorescences often appearing close to the ground on the main trunk. In *G. stipulare* the inflorescences are mostly ramuline, and in addition are fewer-flowered and more strictly cymose. In all other Fijian *Geniostomata*, the inflorescences are either strictly axillary among the leaves, or both axillary and ramuline on juvenile branches.

While we believe that the two species here discussed form a distinct section within *Geniostoma*, we refrain from proposing a formal name, since this should follow a monographic study of the entire genus.

2. Geniostoma stipulare Smith & Stone, sp. nov.

PLATE 1, FIGURE 2; PLATE 2, FIGURES 4–9

Arbor parva ad 5 m. alta, innovationibus et ramulis atque stipulis foliorum petiolis et laminis subtus rufo-pilosis, pilis 3-cellularibus circiter 0.5 mm. longis; ramulis subteretibus vel subcompressis apicem versus 2–5 mm. diametro; stipulis gemmam circumcludentibus per margines petiolorum fere ad basim laminae adnatis anguste oblongis, 1–3.5 cm. longis, caducis; foliis magnitudine disparibus, petiolis 1.5–4.5 cm. longis supra sulcatis subtus rotundatis, laminis ovatis ellipticis vel obovatis, 6.5–34 cm. longis, 3–18 cm. latis, basi cuneato-decurrentibus, apice acuminato-cuspidatis, margine integris, nervis majoribus subtus copiose et areolis sparsius pilosis, costa supra leviter sulcata subtus valde elevata, nervis secundariis utrinsecus 8–15 utrinque paullo elevatis, venulis subtus prominulis; inflorescentiis secus ramos vel ramulos defoliatos enatis conferto-glomeratis sub-sessilibus dichasialibus 15–20-floris, pedunculo ad 1 mm. longo, pedicellis 1–6 mm. longis, bracteolis forma et textura calycis lobis similibus; floribus (videtur pistillatis) in dichasiis congestis trifloris dispositis; calyce cupuliformi, lobis orbiculari-ovatis 1–1.5 mm. longis paulo latioribus 3–5-nervatis; corolla 4.5–5.2 mm. longa ad medium lobata, tubo lobisque extus glabris, tubo intus basi glabro faucibus pilis albis circiter 0.8 mm. longis hirtello, lobis ovatis intus praeter apicem dense hirtellis, nervatio comparate multiplice, corollae quoque loba nervis 3 e basi tubi in lobam adscendentibus praedita, quoque nervo laterali faucibus semel diviso; staminibus in speciminibus nostris forsan abortivis, filamentis deltoideo-ligulatis circiter 0.8 mm. longis pilosis, antheris lanceolato-oblongis apice acutis circiter 1.3 mm. longis et 0.5 mm. latis basi breviter hirtellis, thecis fortasse sterilibus; ovario glabro depresso-globoso 1–1.6 mm. alto 2.5–3 mm. lato, stylo filiformi 2.5–3.5 mm. longo, stigmate globoso diametro

circiter 1.1 mm. papilloso; capsula ovoidea 9-10 mm. longa circiter 4 mm. lata apice apiculata.

Type in the U.S. National Herbarium, Nos. 2192146 and 2336118, collected among hills east of the Navua River, near Nukusere, Province of Serua, Viti Levu, Fiji, alt. 100–200 m., November 2, 1953, by A. C. Smith (No. 9148). Duplicates to be distributed.

ADDITIONAL SPECIMENS EXAMINED:

FIJI: VITI LEVU: Naitasiri or Namosi: Mt. Naitarandamu, near summit, *Gillespie* 3364 (Bish, UC). VANUA LEVU: Thakaundrove: Mt. Ndikeva, in forest on eastern buttress, *Smith* 1860 (Bish, GH, K, NY, UC, US).

DISTRIBUTION: The few specimens known of this species indicate that it is a Fijian endemic restricted to Viti Levu and Vanua Levu. It is a shrub or small, slender tree up to 5 m. high, with relatively large leaves, for the genus, which are sparsely but rather uniformly pubescent on the lower surfaces; it has ramuline inflorescences consisting of congested, subsessile dichasia. The corolla and other floral organs are white, except for the stigma, which is pale yellow.

LOCAL NAME: On the label of *Smith* 1860 the common name is given as *muskarimba*, but this is questionable, since the name often refers to members of the genus *Cyrtandra* (Gesneriaceae), some species of which in fact resemble *G. stipulare* in foliage and superficially in fruit.

This new species, while varying considerably in the size of its leaves, sometimes attains a leaf-size approaching or equalling that of *G. macrophyllum*—two or three times larger than the leaves of most other Fijian *Geniostomata*. However, the pubescence of the leaves and of the inner surfaces of the corolla-lobes, the glabrous ovary, the pilose filaments, the relatively large flowers, and the unusual stipules effectively characterize this species. The inflorescences are noteworthy in that they are borne on older branches, being much contracted dichasia bearing relatively few flowers.

That the relationship of *G. stipulare* is to *G. macrophyllum* is indicated by the large, petiolar stipules and the position of the inflorescences. Together they form a somewhat isolated group; nonetheless, they are nearly as distinct from each other as they both are from their other Fijian congeners. Even the type of trichome that *G. stipulare* produces is distinct; it is usually a three-celled hair, the cells being elongate, and on drying it becomes flattened, the cells then seeming oriented in different planes. These peculiar trichomes, however, are limited to the leaves and innovations; those of the corolla-throat are of the more ordinary type, cylindric and apparently nonseptate.

At mature branchlet-nodes the stipules are lacking, but their occurrence is indicated by the long scars that are left, one on each margin of the petiole, from the base to a point definitely below the blade, but about three-fourths as long as the petiole. Apparently the stipules

are split by the expansive growth of the young leaves, and the remnants are caducous.

There is possibly a third undescribed species of *Geniostoma* of this relationship present in Fiji as yet represented only by a few fragments which are mounted, together with a leaf of *G. macrophyllum*, on a single sheet (*Degener* 14027, from Vanua Levu, in the herbarium of the Arnold Arboretum). If the remaining leaf, which manifestly does not represent *G. macrophyllum*, and the inflorescences do in fact belong together as representing one plant, there seems little doubt that an undescribed species still awaits adequate collecting. The leaf, which is hirtellous beneath with the same three-celled type of trichome found in *G. stipulare*, is as large as those of the type of that species, with a long slender petiole displaying the two linear stipular scars also characteristic of *G. stipulare* (terminating before the base of the blade), but the blade is basally auriculate. The inflorescences, which are greatly elongated and appear to be cauline, bear numerous small congested flowers like those of *G. macrophyllum*. However, they exhibit glabrous ovaries and decidedly mucronulate anthers, in the former character differing from *G. macrophyllum*, and in the latter from *G. stipulare*.

3. Geniostoma confertiflorum Smith & Stone, sp. nov.

PLATE 1, FIGURE 3; PLATE 2, FIGURES 15, 16

Arbor parva 3–10 m. alta praeter corollae partem interiorem ubique glabra, ramulis apicem versus compressis et 2–5 mm. diametro demum teretibus; stipulis intrapetiolaribus in vagina rotundata circiter 1.5 mm. longa apice minute mucronulata conjunctis; foliis magnitudine moderatis, petiolis anguste alatis 9–20 mm. longis, laminis ellipticis vel ovatis, 7–24 cm. longis, 3–13 cm. latis, vulgo 10–23 × 5–12 cm., basi cuneatis vel rotundatis et decurrentibus, apice acuminatis, margine integris, costa supra sulcata subtus elevata, nervis secundariis utrinsecus 8–12 subtus prominulis, venulis obscuris; inflorescentiis axillaribus dichasialibus 5–11-floris, pedunculo communo subnullo haud 1 mm. longo, rhachidibus primariis 1–3 mm. longis bibracteolatis, bracteolis circiter 0.6 mm. longis, pedicellis 2–3 mm. longis in calycem dilatatis; floribus visis videtur hermaphroditis; calyce cupuliformi circiter 2.5 mm. longo, lobis ovatis circiter 1.5 mm. longis 3–5-nervatis; corolla 4–4.7 mm. longa extus glabra, tubo 2–2.4 mm. longo intus basim versus glabro faucibus pilis albis circiter 0.6 mm. longis hirtello, lobis ovatis 2–2.3 mm. longis erectis vel subpatentibus intus praeter basim glabris, nervatio simplice, corollae quoque loba nervo unico subobscuro per tubum ad lobam adscendente praedita, quoque nervo venulum unicum subsimplicem inconspicuum faucibus ferente; staminium filamentis deltoideo-ligulatis 0.3–0.4 mm. longis, antheris anguste

ovoideis circiter 1 mm. longis ubique glabris apice minute apiculatis vel subretusis; ovario depresso-globoso glabro diametro circiter 1 mm., stylo 1–1.3 mm. longo, stigmate oblongo-clavato 1–1.3 mm. longo minute papilloso; capsula late ellipsoidea 7–9 mm. longa apice apiculata, seminibus circiter 1 mm. longis cumulo pulposo flavo-aurantiaco immersis.

Type in the U.S. National Herbarium, No. 2191173, collected in hills north of Wainavindrau Creek, between the Korombasambasanga Range and Mt. Naitarandamu, Province of Namosi, Viti Levu, Fiji, alt. 250–450 m., September 14, 1953, by A. C. Smith (No. 8488). Duplicates to be distributed.

ADDITIONAL SPECIMENS EXAMINED:

FIJI: VITI LEVU: Serua: Mbuyombuyo, near Namboutini, *Tambualewa* 15593 (A, Bish, K, NY, UC, US); hills west of Waivunu Creek, between Ngaloa and Korovou, *Smith* 9240 (US). Naitasiri: Near Tamavua, *Gillespie* 2059 (Bish, NY, UC, US); near Nasinu, *Gillespie* 3637 (Bish, UC, US). Rewa: Near Lami, *Gillespie* 2317 (Bish, UC); Central Road, Suva, *Tothill* 611 (K). OVALAU: Summit of Mt. Ndelaiovalau and adjacent ridge, *Smith* 7381 (US), 7621 (US). NGAU: Slopes of Mt. Ndelaitho, on northern spur toward Navukailangi, *Smith* 7878 (US); hills east of Herald Bay, inland from Sawaieke, *Smith* 7744 (US).

DISTRIBUTION: Endemic to Fiji, thus far known from Viti Levu, Ovalau, and Ngau. The species is noted as arborescent, becoming 3 to 10 m. high, with a trunk up to 5 cm. in diameter; the flowers are white or pale greenish, with the anthers and stigmas sometimes pale yellow. The seeds are noted as yellow. The habitat is in woods or forest, often on ridges or in rocky areas, at elevations from near sea level to 626 m. No local names have been recorded.

This new species, as well as the next one, *G. clavigerum*, is characterized by its clavate stigma; in other Fijian species the stigma is globose or subglobose. In addition, both these species and a third, *G. uninervium*, are similar in that the nervation of their corolla-lobes is relatively simple, consisting of a sparsely or almost unbranched single central nerve.

Of the specimens cited, those from Ngau (*Smith* 7744, 7878) and one from Viti Levu (*Gillespie* 2317) exhibit rather large leaf-blades, which are thin in the former but coriaceous in the latter. Other specimens display considerably smaller leaves, which in respect to size differ little from those of the other Fijian species. Also, an unusual condition is present in *Gillespie* 2059, of which the styles are minutely and sparsely hirtellous rather than glabrous. However, with this one exception, the floral characters of all the specimens agree in size, pilosity, shape, and other characters.

Geniostoma confertiflorum is a species not closely related to those often confused with *G. rupestre*, and it is nearly as well marked a species as *G. macrophyllum* or *G. stipulare*. In superficial characters, such as the average size and shape of the leaves, however, it resembles such

species as *G. rupestre*, *G. macgregorii*, and perhaps glabrate forms of *G. vitiense*—all species of a different group, with globose stigmas and complex corolla-venation. More significantly, *G. confertiflorum* is similar in general appearance to *G. clavigerum* and to *G. uninervium*. The following new species, *G. clavigerum*, differs from *G. confertiflorum* chiefly in its small chartaceous leaves, but also in corolla-venation. From *G. uninervium* the present new species is more easily distinguished by the fainter corolla-venation.

4. Geniostoma clavigerum Smith & Stone, sp. nov.

PLATE 1, FIGURE 4

Arbor parva ad 10 m. alta praeter corollae partem interiorem omnino glabra, ramulis subteretibus apicem versus 1–2 mm. diametro; stipulis intrapetiolaribus in vagina rotundata 1–1.5 mm. alta conjunctis; foliis comparative parvis, petiolis 5–9 mm. longis non alatis, laminis chartaceis ovatis vel elliptico-ovatis, 3–8 cm. longis, 1–3.6 cm. latis, basi obtuso-cuneatis, apice acutis vel subacuminatis, margine integris, costa supra paulo sulcata subtus elevata, nervis secundariis utrinsecus 5–9 utrinque prominulis, venulis obscuris; inflorescentiis axillaribus dichasialibus 3–5 (–9)-floris, pedunculo communo ad 1 mm. longo apice bibracteato, axibus secundariis 1–5 mm. longis ad nodos bibracteatis, pedicellis 1–5 mm. longis infra calycem dilatatis et bracteolatis, bracteis bracteolisque anguste ovatis 0.4–1 mm. longis; floribus (visis videtur hermaphroditis) in dichasiis trifloris dispositis; calyce cupuliformi, lobis ovatis 1–1.5 mm. longis acutis minute ciliolatis 3–5-nervatis; corolla breviter tubulosa extus glabra 4–5 mm. longa, tubo 2–2.5 mm. longo intus basim versus glabro faucibus pilis albis reflexis circiter 0.6 mm. longis hirtello, lobis erectis vel subpatentibus glabris vel basi parce pilosis, nervatio subsimplice, corollae quoque loba nervo unico inconspicuo per tubum adscendente et fere faucibus cum nervulis utrinque 2 lateralibus praedita, nervulis in lobas adscendentibus haud vel obscure ramulosis; staminium filamentis ligulatis, antheris anguste ovoideis circiter 1 mm. longis; ovario depresso-globoso diametro circiter 1 mm., stylo filiformi 1–1.2 mm. longo, stigmate clavato obovoideo vel ellipsoideo circiter 1 mm. longo papilloso; capsula ellipsoidea vel ovoidea 9–10 mm. longa apiculata.

Type in the herbarium of the Bernice P. Bishop Museum, collected on slopes near the base of Mt. Nanggaranambuluta [Lomalangi], near Nandarivatu, Province of Mba, Viti Levu, Fiji, alt. 1,050 meters, in November 1927, by J. W. Gillespie (No. 3916). Duplicate at UC.

ADDITIONAL SPECIMENS EXAMINED:

FIJI: VITI LEVU: Mba: Tholo-i-Nandarivatu, *Gibbs* 724 (BM, K); Mt. Nanggaranambuluta [Lomalangi], *Gillespie* 3782 (Bish, UC), 4334 (Bish, NY, UC).

DISTRIBUTION: Endemic to Fiji, known only from northern Viti Levu, in the elevated area near Nandarivatu at about 1,000 m. or

somewhat higher. Records indicate the species as a small tree 4–10 m. high, with white odorless flowers, occurring in dense wet forests.

Geniostoma clavigerum is very close to the preceding, *G. confertiflorum*, and appears to be a smaller-leaved, smaller-cymed plant. The more complex corolla-venation distinguishes the species, but the smaller leaves and fewer-flowered cymes also appear to be constant. The relatively large flowers and clavate stigmas (whence the name), as well as the corolla-venation, are features which distinguish this species from its other Fijian congeners.

5. Geniostoma uninervium Smith & Stone, sp. nov.

PLATE 1, FIGURE 5; PLATE 2, FIGURES 10–14

Arbor parva ad 10 m. alta praeter corollae partem interiorem ubique glabra vel innovationibus ramulis junioribus stipulis petiolis laminae costisque dorso minute rufo-puberula mox glabrata, ramulis subteretibus vel leviter compressis apicem versus 1–2 mm. diametro; stipulis intrapetiolaribus in vagina rotundata 1–1.5 mm. alta conjunctis; foliis magnitudine moderatis, petiolis 5–9 mm. longis non alatis, laminis chartaceis ovatis, 4.5–15.5 cm. longis, 2–7 cm. latis, plerumque 10–12×3–5 cm., basi rotundatis vel obtuse cuneatis et paulo decurrentibus, apice acuminatis, costa supra leviter sulcata subtus elevata, nervis secundariis utrinsecus 5–9 utrinque prominulis, venulis subobscuris; inflorescentiis axillaribus coarctatis dichasialibus 3–9-floris, pedunculo obsoleto haud 1 mm. longo apice bibracteato axes 1–3 principales gerente, axibus 1–3 mm. longis apice bibracteatis 1–3-floris, pedicellis 2–4 mm. longis plerumque ebracteolatis infra calycem haud dilatatis; calyce cupuliformi, lobis deltoideis circiter 1.5×1.5 mm. minute ciliolatis 3-nervatis, nervo medio fusco lateralibus pallidis; corolla circiter 4 mm. longa urceolata fere ad medium lobata, tubo intus basim versus glabro faucibus pilis albis 0.6–0.7 mm. longis hirtello, lobis demum reflexis, nervatio simplice, corollae quoque loba nervo unico fusco conspicuo lateraliter haud ramuloso praedita; staminium filamentis deltoideo-ligulatis circiter 0.4 mm. longis pilosis, antheris glabris anguste ovatis circiter 0.7 mm. longis minute apiculatis; ovario subgloboso circiter 1.2 mm. diametro apice depresso, stylo filiformi circiter 1 mm. longo, stigmate globoso papilloso circiter 0.7 mm. diametro; capsula ellipsoidea vel obovoidea circiter 10 mm. longa.

Type in the U.S. National Herbarium, No. 2191135, collected in hills north of Wainavindrau Creek, between the Korombasambasanga Range and Mt. Naitarandamu, Province of Namosi, Viti Levu, Fiji, alt. 250–450 m., September 11, 1953, by A. C. Smith (No. 8437). Duplicates to be distributed.

ADDITIONAL SPECIMENS EXAMINED:

FIJI: VITI LEVU: Namosi: Trail between Nanggarawai and Saliandrau, *Gillespie* 3217 (Bish, US). Tailevu: Hills east of Wainimbuka River in vicinity of Ndakui-

vuna, *Smith* 7099 (US). Rewa: Southeastern slope of Mt. Korombamba, *Gillespie* 2295 (A, Bish, UC, US). VANUA LEVU: Thakaundrove: Mt. Mariko, *Smith* 461 (Bish, GH, K, NY, UC, US). OVALAU: Hills west of Lovoni valley, on ridge south of Mt. Korolevu, *Smith* 7527 (US). TAVEUNI: Summit of Uluingalau, *Smith* 896 (Bish, GH, K, NY, UC, US).

DISTRIBUTION: Endemic to Fiji; known thus far from Viti Levu, Vanua Levu, Ovalau, and Taveuni. The plant is arborescent, becoming 5–10 m. high, and occurs at elevations of 100 to 1,200 m. in dense forest or thickets. The corolla and filaments are white or greenish white and the anthers white or yellow.

LOCAL NAMES: "*Mboimboinda*" or "*kavikaloa*" (*Smith* 7099). The former name is a rather general one for species of *Geniostoma* and refers to the characteristic foetid odor.

The relationships of this species are apparently with the two preceding ones, all three sharing a relatively simple pattern of nervation of the corolla-lobes. *Geniostoma uninervium* differs from both *G. confertiflorum* and *G. clavigerum* in its globose stigmas and also in the darker corolla-venation. In the simplicity of this venation it differs from all its Fijian congeners.

6. Geniostoma vitiense Gilg & Benedict in Bot. Jahrb. 56: 542. 1921; A. C. Sm. in Sargentia 1: 97. 1942; Yuncker in Bishop Mus. Bull. 220: 216. 1959.

PLATE 1, FIGURE 6; PLATE 2, FIGURES 21–23; PLATE 3, FIGURES 12–15

Geniostoma crassifolium var. *glaberrimum* Benth. in Journ. Linn. Soc. Bot. 1: 97. 1857.

Geniostoma rupestre var. *puberulum* A. Gray in Proc. Amer. Acad. 4: 33, *nomen.* 1859, in Bonplandia 10: 37, *nomen.* 1862.

Geniostoma rupestre sensu Seem. Fl. Vit. 164. 1866; non J. R. & G. Forst.

Shrub or tree to 12 m. high, the innovations and all young vegetative parts densely pubescent with stiffly erect rufous or cinereous setulose trichomes 0.05–0.2 mm. long, these forming a close and fairly persistent indument on the branchlets, petioles, and ventral side of the costa, and often also on the ventral surface of the blade, the leaves and branches finally glabrate; branchlets somewhat compressed-quadrangular and 1–4 mm. in diameter distally, becoming at length terete; stipules intrapetiolar, forming a short subtruncate sheath 1–1.5 mm. long, soon caducous; leaves petiolate, the petioles 3–10 mm. long, exalate, the blades chartaceous to subcoriaceous, ovate to narrowly ovate or lanceolate-ovate, 2.5–15 cm. long, 1–6.5 cm. broad, commonly about 10×4 cm., subtruncate to nearly subcordate or rounded or broadly acute at base, broadly or narrowly acute to somewhat attenuate or slightly acuminate at apex, entire, glabrous above, pubescent beneath at least on the midrib when young, usually also on veinlets and surfaces, at last glabrate, the costa shallowly sulcate above, raised beneath, the lateral nerves 5–12 per side, commonly 6–8, slightly raised on both surfaces; inflorescences axillary

among the leaves, dichasial, commonly 5–15-flowered, all axes and bracts pubescent or in fruit somewhat glabrate, the peduncle 1–3 mm. long, bibracteate at summit with lanceolate bracts 1.5–2 mm. long, the major axes 2–6 mm. long, bibracteate at nodes, the pedicels 3–6 mm. long, bracteolate or bibracteolate and slightly flared into calyx; flowers borne in triflorous (or irregular) dichasia, slightly sexually dimorphic and apparently gynodioecious, heterostyled; calyx cupuliform, glabrous, the lobes deltoid-ovate, acute or slightly acuminate, 3–5-nerved, marginally ciliolate, about 0.8 mm. long and broad; corolla short-tubular, with spreading or reflexed lobes, glabrous externally, 2.8–3.3 mm. long, the tube half as long, glabrous within at base but above closely pilose around the throat with pale retrorse trichomes 0.2–0.4 mm. long, the lobes glabrous within except at the extreme base with a few trichomes along the veins, ovate, the nervation relatively complex, each lobe supplied by a branching system of nerves consisting of a central main nerve entering the base of the tube and producing 1 or commonly 2 pairs of lateral veins in the upper part of the tube or throat or near the base of the lobe, each lateral vein usually branched once or twice (or rarely thrice), producing brief lateral veinlets, these occasionally obscurely forked near their apices, all ascending in the lobe; stamens inserted at the throat, the filaments deltoid-ligulate, 0.3–0.4 mm. long, retrorse-pilose with trichomes like those of the corolla-throat, the anthers in short-styled flowers narrowly deltoid, about 0.8 mm. long, devoid of pollen, minutely apiculate at apex, the connective pilose at base, the thecae pilose with shorter trichomes at base, the anthers in long-styled flowers fertile, oblong-ovate, 0.8–0.9 mm. long, minutely retuse at apex, the connective glabrous, the thecae basally sparsely hirtellous or glabrous; ovary glabrous, in short-styled flowers large, subglobose, about 1.2 mm. in diameter, the style obsolete or to 0.3 mm. long; the ovary in long-styled flowers smaller, subglobose, about 0.9 mm. in diameter, the style 0.8–0.9 mm. long; stigma papillate, globose, about 0.8 mm. in diameter; capsule ellipsoid, apiculate, 5–9.5 mm. long, 3.5–4.5 mm. broad.

TYPE LOCALITY: Fiji, without precise locality; the type is *Seemann* 301, presumably the specimen deposited in the Berlin herbarium and subsequently destroyed. However, isotypes are available at Kew and the British Museum and are cited below.

DISTRIBUTION: Fiji, Tonga, and Niue, of general occurrence from near sea level to 600 m. altitude in dry forests, secondary forests, open hilly country, or near streams. The species has been recorded as shrubby but also as a tree up to 12 m. high, with a trunk 8 cm. in diameter and curved, pendent branches. The greenish white

flowers produce a markedly foetid odor, which accounts for the Fijian name.

LOCAL NAMES AND USE: Commonly known in Fiji as *mboimboinda*, but also with the following recorded names: *mbatimara* (*Smith* 8966), *mbatimboni* (*Smith* 8405). In Tonga, recorded names are *faifailunga* and *fifilunga*, and on Lifuka (Yuncker), *te'e pilo a Maui*. On Niue, the names *tete* and *teatea* have been recorded by Yuncker. One record of a medicinal use is given, from the Yasawa Group, Fiji, by St. John, where some part of the plant is used as a remedy for stomach-ache.

FIJI: YASAWA GROUP: WAYA: Olo Creek, north of Yalombi, in woods, *St. John* 18018 (Bish, US). VITI LEVU: Mba: North of Lomolomo, *Degener & Ordonez* 13650 (A, Bish, K, NY, UC, US); north of Natalau, *Degener* 15003 (A, Bish, K, NY, UC, US); mountains near Lautoka, *Greenwood* 1237 (A, UC, US); Nandarivatu, *Gibbs* 555 in part, as to pubescent specimen only (BM). Nandronga & Navosa: Near Kalaro, *H. B. R. Parham* 208A (BM); hillsides above Tholo Levu, Nokonoko District, *H. B. R. Parham* 246 (BM). Serua: Hills west of Waivunu Creek between Ngaloa and Korovou, *Smith* 9215 (US), 9274 (US); hills between Navua River and Wainiyavu Creek, near Namuamua, *Smith* 8966 (US); hills east of Navua River near Nukusere, *Smith* 9100 (US). Ra: Vicinity of Rewasa, near Waileka, *Degener* 15461 (A, Bish, K, NY, US). Namosi: Valley of Wainambua Creek, south of Mt. Naitarandamu, *Smith* 8767 (US); hills north of Wainavindrau Creek, between Korombasambasanga Range and Mt. Naitarandamu, *Smith* 8405 (US); near Namosi, in valley of Waindina, *Gillespie* 2619 (Bish, UC). Naitasiri: Near Korosuli, on Wainimala River, *Horne* 978 (K); near Viria, *Meebold* 16499 (K); along Navutu-Nanduna track, *B. E. Parham* 3011 (A); Tholo-i-Suva, *Parks* 20890 (Bish, UC, US); woods near Nasinu, *Gillespie* 3493 (Bish, UC, NY). Naitasiri or Rewa, on border: Mt. Kombalevu, *Parks* 20293A (Bish, US), 20330 (Bish, UC, US). Rewa: Near Suva, *Jeoward* 100 (K). Viti Levu, without precise locality: *Graeffe* 1371 (K). VANUA LEVU: Mbua: Rukuruku Bay, *H. B. R. Parham* 5 (GH). Mathuata: Seanggangga Plateau, in drainage of Korovuli River, near Natua, *Smith* 6642 (A, Bish, K, NY, US); Lambasa, *Greenwood* 490 (K); summit ridge of Mt. Numbuiloa, east of Lambasa, *Smith* 6507 (A, Bish, K, NY, US); Navukuru, south of Lambasa, *Gressitt* 2483 (US). Thakaundrove: Eastern drainage of Yanawai River, *Degener & Ordonez* 14104 (A, Bish, K, NY, UC, US); hills south of Nakula valley, *Smith* 326 (Bish, GH, K, NY, UC, US); Maravu, near Salt Lake, *Degener & Ordonez* 14233 (A, Bish, K, NY, UC, US). Vanua Levu, without precise locality: *U.S. Expl. Exped.* (source of the name *G. rupestre* var. *puberulum*, GH, K, NY, US); *Horne* 614 (K); *Guppy* in 1899 (K); *Tothill* F456 (K). TAVEUNI: Near Waiyevo, *Gillespie* 4634 (Bish); near Wairiki, *Gillespie* 4400.2 (Bish, NY, UC, US). OVALAU: *Milne* 270 (K, type of *G. crassifolium* var. *glaberrimum*); Port Kinnaird, *Seemann* 300 (BM, K). NGAU: Shore of Herald Bay near Sawaieke, *Smith* 8000 (US). Fiji, without definite locality: *Seemann* 301 (isotypes, BM, K, fragment at GH).

TONGA: VAVA'U: *Home* in 1846 (BM); *Barclay* 338A (BM); *Crosby* 229 (K); Talau Hill, *MacDaniels* 1092 (Bish); near upper rim of seaside cliff above Ha'alaufuli on northeastern part of island, *Yuncker* 16101 (US). "Vavau and Lifuka": *Harvey* in 1855 (GH, K). LIFUKA: *Yuncker* 15787 (US). Tonga, without definite locality, "*Capt. Cook*" (BM).

NIUE: East of Alofi village, *Yuncker* 9625 (A, Bish, US), 10092 (Bish, US); near Mutalau village, *Yuncker* 9696 (A, Bish, UC, US).

Geniostoma vitiense was correctly segregated from the inclusive concept of *G. rupestre* by Gilg and Benedict in 1921, but it appears to have been cited since only in the two publications indicated by us above. It is a well marked species, immediately distinguishable from most of its congeners by its close, harsh indument, and more technically by the very short rather dense trichomes of the corolla-throat. Some specimens exhibit a tendency toward glabrescence, while others have harsh persistent indument even on mature parts. The intrapetiolar stipules, the leaves of variable size, and the candelabriform venation of the corolla-lobes are commonplace characters in the genus, but the short trichomes of the corolla-throat and the vegetative pubescence are good distinguishing characters. The leaf-blades, while quite variable, are generally more or less ovate or ovate-lanceolate, often rather broadly rounded or subtruncate at base, and usually acute rather than acuminate at apex. The puberulent dichasial axes are another distinguishing feature of *G. vitiense*, hardly unique, but among the other Fijian species present only in *G. calcicola*, perhaps in *G. insulare*, and sometimes in *G. stenocarpum*.

The sexual dimorphism of the flowers of this species, as yet not very strongly differentiated morphologically, is quite possibly complete in respect to pollen abortion within the anther. As noted in the description, slight divergences in pubescence and in the form of anther exist between the "pistillate" and "perfect" flowers, as well as in the gynoecia. As far as can be made out from the specimens examined, the "perfect" flowers are constant on any one individual, while other individuals produce "pistillate" flowers; thus an incipient, if not an actual, gynodioecism is present. However, sterilization of the staminate organs has not, apparently, been accompanied by sterilization of the pistillate organs in other individuals; and fruits are to be found on both "pistillate" and "perfect" individuals. There may, of course, be some difference in the degree of fertility between these sexual forms, but it is not apparent. The same phenomenon was reported by Valeton for several species of Malaysia. In our area, it is probably common in other species, and definite indications of it have been seen in *G. macgregorii*, while in some species the flowers appear to be all strictly hermaphrodite (as in *G. macrophyllum*). A more intensive study of this problem, carried out in the field, would probably yield some useful information. Perhaps associated with this phenomenon is that of odor; the malodorous flowers of *G. vitiense* and of certain other species are possibly the hermaphrodite rather than the perfect flowers, or vice versa. The odor is such that it probably attracts flies as pollinating vectors. Scentless, or at least not foetid, flowers are known in such species as *G. clavigerum* and perhaps *G. macgregorii*. Such a difference, if it is associated with a difference in the mode of pollination, could be taxonomically significant.

7. **Geniostoma gracile** Rechinger in Rep. Sp. Nov. 6: 325. 1909, in Denkschr. Akad. Wiss. Wien 85: 328. *t. 11*. 1910; Gilg & Benedict in Bot. Jahrb. 56: 544. 1921: Christophersen in Bishop Mus. Bull. 128: 75, pro parte, as to *MacDaniels* 1121 only. 1935.

PLATE 1, FIGURE 7; PLATE 3, FIGURES 9–11

Shrub or small tree with drooping branches, glabrous throughout except for some floral parts, with slender subterete branchlets distally subcompressed and 1–2 mm. thick; stipules intrapetiolar, forming a gently rounded sheath about 1 mm. high; leaves petiolate, the petioles slender, 4–7 mm. long, the blades thin-chartaceous, lanceolate-ovate to elliptic-ovate, relatively narrow, (1.5–) 4–13 cm. long, 1–4.5 cm. broad, rounded to subcuneate and briefly decurrent at base, long-attenuate and sharply acuminate at apex, entire, the costa sulcate above, raised beneath, the lateral nerves 4–10 per side, slightly raised on both surfaces, the veinlets smooth, mostly plane and subevident or obscure; inflorescences axillary among the leaves, dichasial, 3–7 (usually 5–)-flowered, the axes slender and notably elongate, the peduncle 1–7 mm. long, the axes and pedicels 7–17 mm. long, with short bracts about 1 mm. long, the pedicels slightly flared into the calyx; flowers externally glabrous; calyx cupuliform, the lobes deltoid-ovate, acute, 0.7–1 mm. long, 1-nerved to obscurely 3-nerved; corolla about 3.5 mm. long, tubular, divided to middle into suberect or patent deltoid-ovate lobes, the tube closely pubescent within, at throat with pale reflexed trichomes about 0.3 mm. long, those nearer the base of the tube shorter, about 0.1 mm. long, the tube pilose within on the proximal third or half, glabrous distally, the venation relatively complex, that of each corolla-lobe derived from a single central vein ascending from below the tube up to the throat, there producing one or usually two pairs of ascending laterals, these in turn branched laterally once, twice, or even thrice, in the lobe, all the branches ascending and not anastomosing; stamens inserted at throat on short retrorsely pilose deltoid-ligulate filaments about 0.2–0.3 mm. long, the anthers narrowly deltoid-oblong, bluntly tipped, about 0.8×0.35 mm., glabrous; ovary subglobose, about 1 mm. in diameter, narrowed into the filiform glabrous style, this about 1–1.4 mm. long, the stigma clavate-obovoid and subbilobate, papillate, about 0.8–0.9 mm. broad and 1 mm. long; capsule ellipsoid, apiculate, 5–9 mm. long, 4–7 mm. broad.

TYPE LOCALITY: Upolu, Samoa; cited syntypes are *Rechinger* 948 and 1475, of the former of which duplicates are cited below.

DISTRIBUTION: Endemic to Samoa; known only from Savaii and Upolu. The plant is shrubby or becoming a small tree, occurring from near sea level to about 500 m. altitude, in forest or shrubby vegetation. The flowers are white.

LOCAL NAME: *Taipoipo*, according to Gilg & Benedict, who probably derived their information from labels on one of Rechinger's specimens.

SAMOA: Savaii: Coastal thickets, *Reinecke* 532 (K). Upolu: Above U'umapu [Utumapu] ("Utmapu" of Rechinger and Gilg & Benedict), *Rechinger* 948 (isosyntype, BM, US); Vaea, *MacDaniels* 1121 (Bish).

In contrast to Christophersen, who cited a large suite of specimens under this species, we find that only the few specimens cited above represent the species as typified by an isosyntype. Most of the specimens cited by Christophersen under *G. gracile* are here treated as *G. samoense* var. *parviflorum*, a variety imperfectly known to Gilg & Benedict and apparently to Christophersen, and sustained by us as a distinct entity, although the type has not been seen and was presumably destroyed along with the type material of *G. gracile*, *G. vitiense*, and many other species at Berlin. *Geniostoma gracile* appears to be related to *G. macgregorii* and *G. vitiense*, species which also exhibit the very short corolla-throat trichomes characteristic of *G. gracile*. In the narrow, sharply acuminate leaf-blades and the unusually elongate cymose dichasia, *G. gracile* differs from its Fijian relatives and also from most other Samoan *Geniostomata*. However, specimens of *G. samoense* var. *parviflorum* sometimes bear dichasia almost as elongated as those of *G. gracile*; the former appears to be a population commonly found at rather high elevations, and of course it differs from *G. gracile* in its long corolla-throat trichomes.

8. Geniostoma macgregorii (Horne ex Baker) Smith & Stone, comb. nov.

Plate 1, figure 8; Plate 2, figures 17–19

Plectronia macgregori Horne, A Year in Fiji, 266, *nomen*. 1881; Horne ex Baker in Journ. Linn. Soc. Bot. 20: 363. 1883.

Geniostoma rupestre sensu auct. quoad plantas vitienses, pro parte.

Shrub or small tree to 10 m. high, glabrous throughout except for some floral parts; branchlets slender, subterete or slightly compressed and 1–3 mm. in diameter distally; stipules intrapetiolar, forming a subtruncate or gently rounded (or in youngest state, somewhat deltoid) sheath 1–1.5 mm. high; leaves glabrous, petiolate, the petioles 4–16 mm. long, slender, proximally exalate, the blades thick-membranous, chartaceous, or subcoriaceous, when juvenile subglossy, later dull, ovate to elliptic-ovate or oblong-ovate or sublanceolate, 3–16 cm. long, 1–6 cm. broad, commonly about 10×3.5 cm., attenuate, acute, or somewhat rounded at base, briefly decurrent on the petiole, attenuate and acuminate at apex, often very narrowly so or even caudate, entire, the costa sulcate above, slightly elevated beneath, the lateral nerves 5–10 per side, slightly raised on both surfaces, the veinlets evident or obscure, plane; inflorescences axillary among the leaves, dichasial, usually 5–15-flowered, rarely to 20-flowered, all the axes glabrous, the peduncle stout, flattened, 1–4 mm. long, bibracteate at summit with lanceolate bracts 1–1.5 mm. long, the major axes slender, 2–6 mm. long, bibracteate at nodes, the pedicels 2–6 mm. long, slender,

flared and bracteolate below the calyx; flowers borne in triflorous (or near the peduncle uni- or biflorous) dichasia, glabrous externally; calyx cupuliform, the lobes deltoid-ovate, 1–3 (rarely 5–)-nerved, about 1 mm. long, as broad or nearly as broad; corolla short-tubular, slightly urceolate, with reflexed lobes, 3–4 mm. long, divided to middle, the tube glabrous within basally, above to throat and on base of lobes closely pilosulous with short retrorse trichomes 0.1–0.25 mm. long, the lobes ovate, basally pilosulous like the throat, distally merely pustulous with pustules 0.05 mm. high, at the extreme apex glabrous, the venation relatively complex, each corolla-lobe supplied by three main nerves entering the tube already distinct, or diverging in the lower part of tube, ascending to throat and into the lobe, producing 2–4 short ascending (rarely forked) lateral nerves; stamens inserted at throat, the filaments deltoid-ligulate, about 0.4 mm. long, closely pilosulous with short retrorse trichomes like those of the throat, the anthers narrowly oblong-deltoid, about 0.8 mm. long, acute, glabrous; ovary glabrous, subglobose, about 1.4 mm. high and 1.8 mm. broad, the style glabrous, filiform, 1.2–1.5 mm. long in long-styled flowers, 0.7–0.9 mm. long in short-styled flowers, the stigma globose; capsule narrowly ellipsoid or narrowly ovoid, 7–13 mm. long, 3–4.5 mm. broad.

TYPE LOCALITY: Ovalau, Fiji; the type is *Horne* 261, cited below.

DISTRIBUTION: Known only from Fiji and Tonga. The plant is a slender shrub or small tree 3–10 m. high, bearing flowers with a greenish white or pale green corolla and a white stigma; the fruit is green without, the inner pulp orange. The habitat is noted as dense or open forest, or near the margins of forest, from near sea level to 900 m. altitude, mostly between 50 and 200 m. altitude.

LOCAL NAMES: Very rarely noted, although numerous specimens are at hand; *mboimboinda* on a few specimens from Vanua Levu; Graeffe's collection from Ovalau bears the name *mbatimbona*. Three collectors note that the foetid odor common to *G. vitiense* is not present, and indeed one states "odorless" (*Greenwood* 541A); another states that there is an odor, but not a foetid one (rather, says the Tothill label, a "horsy" scent). These data, in conjunction with the rare usage of the name *mboimboinda*, may indicate that the plants are scentless or at least not malodorous.

FIJI: VITI LEVU: Mba: Mt. Evans, *Greenwood* 388 (K); near Lautoka, *Greenwood* 49 (K); northern slopes of Mt. Namendre, east of Mt. Koromba ("Pickering Peak"), *Smith* 4554 (A, Bish, K, NY, US). Nandronga & Navosa: Near Mbelo and Vatukarasa, *Degener* 15296 (A, K, NY). Serua: Hills west of Waivunu Creek, between Ngaloa and Korovou, *Smith* 9318 (US), 9469 (US); vicinity of Ngaloa, *Degener* 15071 (A, Bish, K, NY, UC, US); near Vatutavathe, *Degener* 15206 (A, Bish, K, NY, UC, US); hills between Wainiggere and Waisese Creeks, between Ngaloa and Wainiyambia, *Smith* 9357 (US). Namosi: Coastal hills, *Greenwood* 541A (A). Tailevu: Uthunivanua, *McKee* 2817 (US). Naitasiri:

Near Viria, on Rewa River, *Meebold* 16507 (Bish); woods beyond Tamavua, Gillespie 2151 (Bish), 2170 (A, Bish, NY, UC, US); Wainimbuku River area, on ridge near Nasinu river, *Shradha Nand* [Fiji Dept. Agric. No.] 7358 (US); near Nasinu, *Gillespie* 3528 (Bish, NY, UC); Suva Pumping Station, *Degener & Ordonez* 13757 (A, US). Rewa: Near Naikorokoro River west of Suva, *Meebold* 21943 (Bish); Mt. Korombamba, *H. B. R. Parham* 84 (BM); southeastern slopes of Mt. Korombamba, *Gillespie* 2230 (Bish, UC); summit of Mt. Korombamba, *Gillespie* 2395 (Bish, UC); lower slopes of Mt. Korombamba, *Vaughan* 3327 (BM, K); near Suva, *Tothill* 477 (Bish, K), 623 (K), *Meebold* 16436 (K), 21387 (BM, NY); Central Road, Suva, *Tothill* 625 (Bish); mouth of Rewa River, *Guppy* in 1899 (K). KANDAVU: Hills above Namalata and Ngaloa Bays, *Smith* 132 (Bish, GH, K, NY, UC, US). VANUA LEVU: Mathuata: Hills near Lambasa, *Greenwood* 511 (K), 541 (K); southern slope of Mt. Numbuiloa east of Lambasa, *Smith* 6398 (A, Bish, K, NY, US), 6576 (A, Bish, K, US). Thakaundrove: Southwestern slope of Mt. Mbatini, *Smith* 668 (Bish, GH, K, NY, UC, US). OVALAU: *Graeffe* 1612 (K); vicinity of Levuka, *Horne* 96A (GH, K); "mountains of Ovalau," *Horne* 261 (GH, K type). KORO: *Tothill* 612 (Bish in part, K). MATUKU: *Milne* 128 (K), 128 bis (K). KAMBARA: Central wooded basin, *Bryan* 504 (Bish). Fiji Islands, without definite locality, *U. S. Expl. Exped.* (US).

TONGA: VAVA'U: Near Neiafu, *Setchell* 15656 (UC).

This species, frequent in Fiji, was described in very general terms by Baker (and not at all by Horne); it provides not the only illustration of confusion between *Geniostoma* and *Plectronia* (i.e. *Canthium*, Rubiaceae), as evidenced by *G. niinoanense* Kanehira (=*Canthium barbatum* (Forst. f.) Seem. var. *korrorense* (Valeton) Fosberg, the variety based on *Plectronia korrorensis* Valeton). However, there is no question as to the identity of Horne's specimen, and therefore his specific epithet, corrected in accordance with Rec. 73C of the International Code of Botanical Nomenclature, must be used.

Although material here cited has generally been previously identified as *G. rupestre*, it is less closely related to that species than it is to *G. vitiense*, even though the pubescence of the latter gives a superficial impression of difference that is not entirely warranted. The short trichomes of the corolla-throat are a constant feature of *G. macgregorii* and serve to distinguish it at once from the New Hebridean *G. rupestre*. From *G. vitiense*, *G. macgregorii* differs in being glabrous and in having its leaf-blades relatively more narrow (in most specimens) and usually long-acuminate; in floral characters the two are very similar. The remarks on sexual dimorphism given under *G. vitiense* also apply here.

Only the single specimen cited above from Tonga carries the known distribution of *G. macgregorii* beyond Fiji; this specimen, while not entirely typical, cannot be referred to any other species occurring in Tonga and we believe it to be correctly placed here. Outside of our area, *G. batanense* Merr., of the Philippines, is somewhat similar in general aspect to *G. macgregorii*, but it has externally puberulent flowers and a setulose style.

9. Geniostoma calcicola A. C. Sm. in Sargentia 1: 99. 1942.

PLATE 1, FIGURE 9; PLATE 2, FIGURE 24

Geniostoma sp. A. C. Sm. in Bishop Mus. Bull. 141: 125. 1936.

Scandent shrub to 50 cm. high, with slender terete fusco-cinereous branchlets at first densely short-setose with pale, conic-tapered, several-celled setae; stipules intrapetiolar, forming a short broadly ovate sheath; leaves densely puberulent, petiolate, the petioles 3–5 mm. long, the blades chartaceous, elliptic or oblong-elliptic, 3.5–5 cm. long, 1.5–2.5 cm. broad, obtuse at base, rounded or slightly emarginate or minutely mucronulate at apex, entire, with slightly recurved margins, pilose on both surfaces, the trichomes about 0.3 mm. long, the costa shallowly sulcate above, raised beneath, the lateral nerves 4–6 per side, shallowly sulcate above, slightly raised beneath, the veinlets obscure; inflorescences axillary, dichasial, slender, open, 5 (rarely 9–)-flowered, the peduncle 1 mm. long, the pedicels 2–5 mm. long, the nodes bibracteate, the flowers bracteolate just below the calyx, all the axes sparingly setulose; flowers borne on relatively long slender pedicels scarcely flared at apex; calyx cupuliform, glabrous except for the ciliolate margin, the lobes acute, ovate-deltoid, 1.2–1.5 mm. long, 1–3-nerved; corolla short-tubular, 3.5–4 mm. long, glabrous externally, the tube about 2.5 mm. in diameter, glabrous within at base, pilose at throat with white trichomes about 0.8 mm. long sparsely but uniformly disposed around throat, the lobes about 1.5 mm. long, ovate, reflexed, glabrous except at extreme base, the venation pinnate, each corolla-lobe supplied by one main nerve branched just below the lobe or sometimes toward base of tube into 2 main lateral nerves, all ascending into the lobe and there unbranched or with a few short free laterals; stamens inserted at throat, the filaments ligulate, about 0.4 mm. long, sparsely pilose, the anthers oblong, basally cordate, apically obtuse, about 1 mm. long; ovary glabrous, depressed-subglobose, about 1.3 mm. in diameter, the style filiform, about 1 mm. long, glabrous, the stigma subglobose to somewhat obcordate, about 0.8 mm. in diameter, papillate; capsule unknown.

TYPE LOCALITY: Fulanga, Fiji; the type is *Smith* 1116, cited below.

DISTRIBUTION: Known only from the type collection, collected on cliff face in limestone formation; the corolla is white. The other specimens tentatively referred to *G. calcicola* in the original publication are now accounted for under *G. insulare*.

FIJI: FULANGA: Near Monothaki, near sea level, *Smith* 1116 (Bish, GH type, K, NY, UC, US).

Although the occurrence of this species on other islands of Lau may be suspected, at present we do not have a single collection other than

the type referable to it. Its closest relatives are *G. crassifolium* Benth., of the Isle of Pines, and *G. insulare*, described below. Relationships among the three species may be indicated in the following key:

Leaf-blades puberulent on both surfaces.
  Ovary and style hirtellous, the style 0.3–0.5 mm. long, the stigma clavate; anthers about 1.2 mm. long; dichasia closely hirtellous; leaf-blades up to 7×4 cm . . . . . **G. crassifolium**
  Ovary and style glabrous, the style 0.8–1 mm. long, the stigma obovoid or subglobose; anthers about 0.9 mm. long; dichasia sparsely hirtellous; leaf-blades up to 5×2.5 cm . . . . . **G. calcicola**
Leaf-blades glabrous or puberulent only beneath . . . . . **G. insulare**

Reference of Tongan plants to *G. calcicola* in Yuncker's *Plants of Tonga* (in Bishop Mus. Bull. 220: 215. 1959) was based, we now believe, on too inclusive a concept, and these plants are now cited under *G. insulare*.

10. Geniostoma dictyoneurum Smith & Stone, sp. nov.

PLATE 1, FIGURE 10

Arbor gracilis ad 7 m. alta praeter corollae partem interiorem omnino glabra, ramulis gracilibus apicem versus 1–2 mm. diametro et subteretibus vel obscure quadrangularibus; stipulis intrapetiolaribus in vagina rotundata vel subtruncata 1–1.3 mm. alta conjunctis; foliis magnitudine moderatis, petiolis 8–12 mm. longis, laminis membranaceis vel tenuiter chartaceis ovatis, 7–12 cm. longis, 3.5–7 cm. latis, basi rotundatis vel subtruncatis et in petiolum subito cuneato-decurrentibus, apice rotundatis, margine integris, costa supra sulcata subtus conspicue elevata, nervis lateralibus utrinsecus 4–10 utrinque prominulis, venulis obscuris; inflorescentiis axillaribus vel ramulis paulo infra folia enatis dichasialibus, pedunculo crasso 1–2 mm. longo apice bibracteato axes 1–3 principales graciles nodis bibracteatos 4–6 mm. longos gerente, bracteis 0.5–1 mm. longis, axibus 3–9-floris, floribus 1–3 in dichasiis dispositis, pedicellis gracilibus 1–3 mm. longis infra calycem dilatatis et bracteola calycem adpressa ornatis; calyce cupuliformi, lobis deltoideis 0.6–0.8 mm. longis minute ciliolatis uninervatis vel interdum inconspicue 3-nervatis; corolla circiter 4 mm. longa ad medium lobata, tubo faucibus pilis circiter 0.5 mm. longis hirtello, lobis ovatis basim versus interdum parce hirtellis, nervatio intricato, corollae quoque loba nervis 3 e basi tubi in lobam adscendentibus praedita, quoque nervo venulis lateralibus pluribus tenuibus in reticulum laxum conjunctis ornato; staminium filamentis ad 0.2 mm. longis copiose hirtellis, antheris anguste deltoideo-ovoideis circiter 0.9×0.4 mm. apice acutis basi haud parce hirtellis; ovario depresso-globoso circiter 0.8 mm. lato, stylo filiformi ad 0.5 mm. longo, stigmate

subgloboso papilloso circiter 0.5 mm. lato; capsula subglobosa vel ate ovoidea, 5–6 mm. longa, 4.5–5.5 mm. lata, apice apiculata.

Type in the U.S. National Herbarium, No. 2190641, collected among the hills east of Herald Bay, inland from Sawaieke, Ngau, Fiji, alt. 300–450 m., June 18, 1953, by A. C. Smith (No. 7814). Duplicates to be distributed.

ADDITIONAL SPECIMENS EXAMINED:

FIJI: KORO: Rocky thicket at sea level on east coast, *Smith* 1037 (Bish, GH, K, NY, UC, US).

DISTRIBUTION: Endemic to Fiji, and known only from Ngau and Koro. The plant is recorded as a slender tree 5–7 m. high, growing in forest from sea level to 450 m. altitude, the flowers with corolla and filaments pale green or white, the anthers white.

LOCAL NAME: *Mboimboinda* (Koro).

Geniostoma dictyoneurum, as the name implies, exhibits anastomosing venation of the corolla-lobes, a character found very rarely in other species. The leaf-blades are rather broadly ovate, apically blunt or rounded, noticeably thin-membranous, and relatively large for the genus, with 4–10 lateral nerves on each side of the midrib. The pilosity of the corolla inner surface is densest on the filaments; on the corolla-throat it is sparser and covers a narrower band. In this respect there exists a certain resemblance to specimens of *G. vitiense*, which occasionally shows a similar variability in corolla-indument. The completely glabrous vegetative parts of the present species readily distinguish it from *G. vitiense*. A resemblance to *G. macgregorii* may also be noted, but the long corolla-throat hairs of *G. dictyoneurum*, and of course the anastomosing corolla-lobe venation, quickly differentiate it. Perhaps the closest relative of *G. dictyoneurum* is *G. insulare*, at least the form with subglobose capsules; in *G. dictyoneurum* the capsules are also regularly sphaeroidal rather than elongated.

11. Geniostoma fleischmannii Rechinger in Rep. Sp. Nov. 7: 17, as *G. fleischmanni*. 1909, in Denkschr. Akad. Wiss. Wien 85: 329. *t. 10*. 1910; Gilg & Benedict in Bot. Jahrb. 56: 545. 1921; Christophersen in Bishop Mus. Bull. 128: 175, as *G. fleischmanni*. 1935. PLATE 1, FIGURE 11

Shrub or small tree 3–4 m. high, glabrous throughout except for some floral parts; branchlets slender, gray-brown, markedly quadrangular and narrowly winged, distally 1–3 mm. thick; stipules intrapetiolar, forming a truncate sheath about 1 mm. long; leaves glabrous, petiolate, the petioles 2–7 mm. long, the blades oblanceolate or narrowly elliptic, 4–12 cm. long, 1.5–3.5 cm. broad, attenuate-decurrent or sometimes acute and decurrent at base, acute to acuminate at apex, the costa shallowly sulcate above, slightly raised beneath, the lateral nerves 6–12 but usually 9 or 10 per side, slightly raised on both surfaces, the veinlets obscure; inflorescences axillary among the leaves,

dichasial, usually 5–10-flowered, the peduncle flattened, subobsolete or to 1.5 mm. long, the axes and pedicels 4–9 mm. long, bracteate with bracts to 1.5 mm. long, the pedicels bracteolate and flared just below calyx; flowers slenderly pedicellate; calyx cupuliform, the lobes deltoid, about 1 mm. long and 0.8 mm. broad, 1–3-nerved; corolla 4.5–5 mm. long, the tube 2.5–2.7 mm. long, glabrous without, glabrous within at the extreme base but retrorse-pilose above to throat with trichomes 0.7–0.9 mm. long, the lobes 1.9–2.3 mm. long, glabrous distally, deltoid-ovate, the venation complex, each lobe supplied by one main nerve, this usually narrowly divaricate in the tube, ascending and branching into the lobe, producing 2–4 ascending lateral branch-nerves, these occasionally briefly branched; stamens inserted at throat, with short pilose filaments 0.3–0.5 mm. long, the anthers deltoid, blunt-tipped, about 0.7 mm. long; ovary glabrous, about 1.5 mm. high and 1.8 mm. broad, the style filiform, glabrous, about 1 mm. long, the stigma subglobose, subbilobate, about 0.9 mm. in diameter; capsule ellipsoid, 7–8 mm. long, about 4 mm. broad, short-apiculate.

TYPE LOCALITY: Savaii, Samoa; the type is *Rechinger* 1648, presumably deposited at Berlin and subsequently destroyed. We have seen no isotypes, but the species is very well illustrated and easily recognized.

DISTRIBUTION: Endemic to Samoa; apparently known only from Savaii. It is said to be a shrubby species becoming a small tree 4 m. high, with markedly 4-angled branchlets and with white flowers, occurring at high elevations (1030 m. according to Christophersen & Hume), or in "sunny openings near Asau" (Rechinger).

SAMOA: SAVAII: Forest above Matavanu, *Christophersen & Hume* 2124 (Bish, NY, UC, US).

Characters that amply distinguish *G. fleischmannii* from other Samoan species, and in combination from its congeners throughout the Pacific, are its relatively large corollas, its candelabriform corolla-lobe venation of an unusual type (consisting of a dichotomous main nerve with several laterals rather than being 3 or 5-nerved), its long, narrow, usually oblanceolate leaf-blades, and its 4-winged branchlets.

12. Geniostoma stenocarpum A. C. Sm. in Sargentia 1: 98. 1942.

PLATE 1, FIGURE 12; PLATE 3, FIGURES 7, 8

Shrub or small tree to 4 m. high, with at first often minutely pubescent but soon glabrate slender subterete branchlets; stipules intrapetiolar, forming a short rounded sheath; leaves petiolate, the petioles 2–6 mm. long, the blades lanceolate or narrowly ovate, 4–7.5 cm. long, 1.2–2.7 cm. broad, attenuate and decurrent or merely acute at base, or very rarely subtruncate, narrowly acute to slightly

acuminate at apex, entire, the costa slightly sulcate above, raised beneath, the lateral nerves 4–7 per side, prominulent, the veinlets mostly obscure; inflorescences glabrous or sometimes at first minutely pubescent and soon glabrate, axillary among the leaves, 5–12(–18)-flowered, dichasial, compound dichasial, or often irregular, the peduncle 1 mm. long or less, the major axes 3–6 mm. long, the nodes bibracteate (sometimes with only 1 or with no bract), the pedicels 2–5 mm. long, bracteolate, the bracteoles about 0.5 mm. long; calyx cupuliform, the lobes deltoid-ovate, acute or short-acuminate, 1–3-nerved, the margins ciliolate; corolla short-tubular, 2.5–3.5 mm. long, glabrous externally, divided to middle, the tube glabrous within basally, sparsely hirtellous at throat with trichomes about 0.4 mm. long, similarly hirtellous in a narrow median horizontal band and on filaments (but glabrous between filaments in upper portion), the lobes ovate, glabrous, the venation relatively complex, each corolla-lobe supplied by 3 nerves with several lateral branches in the lobe, derived from a single main nerve entering the tube and producing two main lateral nerves in the throat; stamens inserted at throat, the filaments narrowly deltoid-ligulate, about 0.6 mm. long, pilose, the anthers glabrous except at extreme base, obtuse or with a minute mucronulate apex, ovate-oblong, 0.8–0.9 mm. long; ovary glabrous, subglobose, about 1 mm. in diameter, the style filiform, glabrous, short to nearly obsolete, 0.3–0.7 mm. long, the stigma subglobose, about 0.5 mm. in diameter, papillate; capsule ellipsoid, 7–10 mm. long, 2.5–3.5 mm. wide, apiculate by the stylar remnant, subtended basally by the persistent calyx.

TYPE LOCALITY: Nandarivatu, Viti Levu, Fiji; the type, *Degener & Ordonez* 13591, is cited below.

DISTRIBUTION: Endemic to Fiji and thus far known only from Viti Levu, where it appears quite frequent at middle elevations. It has been recorded as a shrub or small tree up to 4 m. high, occurring in or on borders of dense forest at elevations up to 1150 m. and only rarely as low as 150 m.; the flowers are greenish or white.

LOCAL NAMES: *Mbati-mbati* (*Gillespie* 3170); *mbuimbuita* (*Smith* 4993, 6020); *mbatimara* (*Smith* 5062).

FIJI: VITI LEVU: Mba: Nandarivatu and vicinity, *Gibbs* 555, pro parte (BM), *Tothill* 626 (K), *Gillespie* 3170 (Bish), 4280 (Bish, UC), *Degener & Ordonez* 13591 (A type, Bish, K, NY, UC, US), 13592 (A, Bish, K, NY, UC, US), 14314 (A, Bish, K, NY, UC, US); slopes of escarpment north of Nandarivatu, *Smith* 6020 (A, Bish, K, NY, US); Mt. Ndelaiyoö, on escarpment west of Nandarivatu, *Smith* 5062 (A, Bish, K, NY, US); ridge between Mt. Nanggaranambuluta and Mt. Namama, east of Nandarivatu, *Smith* 4993 (A, Bish, K, NY, US); slopes of Mt. Tomanivi [Mt. Victoria], *Smith* 5226 (A, Bish, K, NY, US); hills between Nandala and Nukunuku Creeks, along trail from Nandarivatu toward Lewa, *Smith* 6152 (A, Bish, K, NY, US). Nandronga & Navosa: Northern portion of Rairaimatuku Plateau, between Nandrau and Rewasau, *Smith* 5394 (A, Bish, K, NY, US). Serua: Banks of Navua River, at Namata Rapids, *Gillespie* 2941 (Bish, UC).

The available specimens fall into three fairly well marked forms that appear not significant enough to merit names: a narrow-leaved glabrous form, a narrow-leaved puberulent form, and a glabrous form with comparatively broad, ovate leaf-blades. The first of these includes the type collection and most of the cited specimens. Only three collections (*Degener* 14314 and *Gillespie* 2941 and 4280) show a marked and fairly persistent puberulence on the branchlets; a minute indument is frequent on the innovations but is usually soon lost. One puzzling specimen, *Smith* 6020, seems to have both glabrous and persistently puberulent branchlets on one tree. The third form, with leaf-blades ovate and rounded to subtruncate at base, is represented by *Gibbs* 555 and *Smith* 5394. Association of these three forms with particular habitats or altitudes does not at this time seem to be noteworthy.

The closest relationship of *G. stenocarpum* appears to be with *G. rupestre*, of the New Hebrides, and less notably with *G. insulare*. The small and predominantly lanceolate leaf-blades give a very distinct aspect to *G. stenocarpum*. Although corolla-lobe venation is not an entirely dependable criterion of relationship, in this respect *G. stenocarpum* is closer to *G. insulare* than to *G. rupestre*, in which the lobe-supplying nerve usually divides at or near the base of the corolla-tube.

The flowers of *G. stenocarpum* are noted as foetid only by Gibbs, whose No. 555 is a mixture with *G. vitiense*; her comment may apply to the latter species, which is reported by various collectors as having malodorous flowers.

13. Geniostoma samoense Reinecke in Bot. Jahrb. 25: 666. 1898; Rechinger in Denkschr. Akad. Wiss. Wien 85: 328. 1910; Gilg & Benedict in Bot. Jahrb. 56: 543. 1921; Setchell in Carnegie Inst. Publ. 341: 59. 1924.
PLATE 1, FIGURE 13

Small tree to 10 m. high or shrub, glabrous throughout except the axes of the inflorescence and some floral parts, or the innovations at first minutely pubescent, soon glabrate; branchlets distally 1–3 mm. in diameter, subterete or somewhat compressed-quadrangular, in age terete; stipules intrapetiolar, forming a subtruncate or gently rounded sheath 1–2 mm. high; leaves petiolate, the petioles 5–15 mm. long, exalate, the blades chartaceous, ovate to broadly ovate, 3–18 cm. long, 1.5–9 cm. broad, rounded or obtuse-cuneate and decurrent at base, obtuse to acuminate at apex, entire, the costa sulcate above, raised beneath, the lateral nerves 5–10 per side, slightly raised on both sides, the veinlets manifest or somewhat obscure, not raised; inflorescences axillary among the leaves, dischasial, the dichasia strict or often irregularly branching, 5–15-flowered, commonly 9-flowered, the peduncle about 1 mm. long and 0.7 mm. thick, bibrac-

teate at summit, the major axes 2–5 mm. long, the pedicels 1–3 mm. long, bibracteolate at nodes or sometimes irregularly 1- or 2-bracteolate, the bracteoles when opposite continuous across the node, sheathing, all the axes minutely puberulent with short blunt trichomes no more than 0.03 mm. in length; calyx 1.3–1.6 mm. long, the lobes equal in length to the tube, broadly deltoid, about 0.7 mm. long and 1 mm. wide, marginally ciliolate, 3-nerved (rarely obscurely so); corolla 2.5–3.3 mm. long, the tube 1.2–1.8 mm. long, glabrous without, glabrous within in the lower half, pilose in the upper half to the throat with white trichomes 0.45–0.7 mm. long, the lobes glabrous or pilose only at extreme base, the venation comparatively complex, each corolla-lobe supplied by 3 main nerves diverging near base of tube and branching laterally near throat, all ascending into the lobe, there with brief lateral branches or none; stamens inserted at throat, the filaments pilose, ligulate, about 0.3 mm. long, the anthers ovate, acute or obtuse, about 0.7 mm. long and 0.5 mm. broad; ovary glabrous, subglobose, about 1 mm. in diameter, the style about 0.2 mm. long, glabrous, the stigma depressed-globose or subglobose, papillate, 0.7–1 mm. in diameter; mature capsule ellipsoid-obovoid, briefly apiculate by the stylar remnant, the lobes dehiscent-recurved, 8–10 mm. long, 4–5 mm. broad; seeds ovoid with a concave hilum, the testa minutely papillate, about 0.06 mm. thick, the papillae no more than 0.015 mm. high, orange in life.

Geniostoma samoense is a species of the alliance of *G. rupestre*, differing chiefly in the puberulent dichasia, the relatively broader capsules, and the larger, broader, usually more obtuse leaf-blades. The venation of the corolla-lobes is very similar to that of *G. rupestre*, there being some variability within each species as to the height in the corolla-tube of the point of divergence of the three main nerves. The venation of the sepals is generally 3-nerved, although the two lateral nerves are sometimes short and obscure. The dichasia are distinctly but minutely puberulent with trichomes no more than 0.03 mm. long, which are usually persistent even on fruiting specimens.

Several specimens cited by Christophersen (in Bishop Mus. Bull. 128:176. 1935) as *G. rupestre* are here referred to *G. samoense*, a species not considered by Christophersen in identifying his material. There is no indication that Christophersen believed Reinecke's species a synonym of *G. rupestre*, but this was possibly the case. We are satisfied that the two entities amply merit specific recognition.

The available material of *G. samoense* represents two varieties, which may be differentiated as follows:

Leaf-blades usually 8–18×4–9 cm., rounded at base, obtuse to obtusely acuminate at apex; anthers blunt at apex; stigma globose; plants of low elevations. **var. samoense**

Leaf-blades usually 3–11×1.5–4.5 cm., cuneate at base, long-acuminate at apex; anthers minutely mucronulate; stigma depressed; plants usually of mountain forests. . . . . var. **parviflorum**

13a. Geniostoma samoense var. **samoense**

PLATE 2, FIGURES 25, 27, 28; PLATE 3, FIGURES 1–4

Geniostoma rupestre var. *macrophyllum* A. Gray in Proc. Amer. Acad. 4: 33, *nomen.* 1859.

Leaf-blades large, relatively broad, rounded at base, obtuse to obtusely acuminate at apex, comparatively thin in texture; bracts 1–1.3 mm. long; anthers blunt at apex; stigma globose, the style short.

TYPE LOCALITY: Samoa; the precise locality and the identity of the holotype are uncertain, since Reinecke cited his own collection (275) from Upolu and three Graeffe specimens (245 and 1393 from Upolu, and 1613 from Savaii). Rather than designate a lectotype at this time we prefer to consider the four collections as syntypes; duplicates of two of them (Graeffe 1393 and 1613) have been seen and are cited below as isosyntypes.

DISTRIBUTION: On the basis of available material, this typical variety is seen to occur on several islands of Samoa and also on Uvea, Wallis Islands. It is recorded as a shrub or small tree, with white flowers; the seeds are brown, embedded in orange pulp. Habitats reported are swampy forest near the coast, thickets on rocky bluffs, near lava fields, or in *fau* (*Hibiscus tiliaceus*) forest, from altitudes of near sea level to 680 m. (summit of Mt. Fao).

LOCAL NAMES: *Taitai-ipu* (Christophersen); *taipoipo* (Reinecke, on Upolu); *fatimatao* (Powell, on Upolu); *laumafatifati* (Setchell, on Tutuila, and also Powell).

SAMOA: SAVAII: Matautu, *Vaupel* 222 (Bish, K, NY, US); between Letui and Aopo, *Christophersen* 906 (Bish); Matavanu lava field, *Christophersen & Hume* 1898 (Bish); Safotu-Manase, *Christophersen & Hume* 2451 (Bish, UC, US); near Salaeula, lava flow of 1905–1911, *Christophersen* 2467 (Bish, NY); without precise locality, *Graeffe* 1613 (K isosyntype). UPOLU: Summit of Mt. Fao, *Christophersen* 556 (Bish, NY, UC); without precise locality, Graeffe 18 (BM), 1393 (K isosyntype), 1614 (K). Tutuila or Upolu: *Powell* 257 (K). TUTUILA: Near Nuuli, *Setchell* 117 (Bish, UC); Breakers Point, *Seale* in 1929 (NY); Pango Pango harbor, *Diefenderfer* 29 (Bish); Pango Pango and vicinity, *Yuncker* 9336 (Bish), *Kuntze* 23007 (NY), *Meebold* 12646 (Bish, K), *Setchell* 264 (UC), *Collarino* (*Setchell* no.) 578 (UC). OFU: *Yuncker* 9453 (Bish, US), 9477 (Bish, UC, US). TAU: South of Siufaga, *Yuncker* 9005 (A, Bish, US); near Siufaga, *Yuncker* 9192 (Bish). Samoa, without locality, *Graeffe* s.n. (GH); *U.S. Expl. Exped.* (source of the name *G. rupestre* var. *macrophyllum*, GH, NY, US).

UVEA (Wallis Islands): Without other locality, *Graeffe* 42 (BM).

13b. Geniostoma samoense var. parviflorum Reinecke in Bot. Jahrb. 25: 666, as var. *parviflora*. 1898; Gilg & Benedict in Bot. Jahrb. 56: 544, as var. *parviflora*. 1921.

PLATE 2, FIGURE 26; PLATE 3, FIGURES 5, 6

Leaf-blades comparatively small, usually 3–11×1.5–4.5 cm., cuneate at base, long-acuminate at apex, pale beneath, with obvious venation; anthers minutely mucronulate with a tip about 0.1 mm. long; stigma depressed, about 0.7 mm. in diameter, broader than high.

TYPE LOCALITY: Upolu, Samoa; the type is *Reinecke* 555, which we have not seen. Gilg & Benedict mentioned the specimen (in 1921) as moldy and useless, but nevertheless they opined that it might represent a distinct species.

DISTRIBUTION: Samoa, known only from Savaii and Upolu; the material available to us is all from the former island. The variety is recorded as a small tree or shrub up to 10 m. high, with white flowers and green fruits. It usually occurs between 1,000 and 1,400 m. altitude, but on occasion as low as 200 m.

SAMOA: SAVAII: Matavanu crater, *Christophersen* 609 (Bish, US); Matavanu lava field, *Christophersen & Hume* 1878 (Bish, UC, NY); above Matavanu, *Christophersen & Hume* 2200 (Bish, NY); Letui, *Christophersen* 775 (Bish, UC, US); above Salailua, *Christophersen* 2675 (A, Bish, UC, US), 3118 (Bish, UC, NY); Siuvao-Auala, *Christophersen* 3375 (Bish).

Although there is a strong difference in general aspect between the two varieties here recognized, no significant floral characters appear to distinguish them. The flowers in both are about the same size, and why Reinecke selected the varietal epithet "*parviflora*" is not clear. His original description of the variety is not very helpful, but it seems definitely to refer to the small-leaved form with long-acuminate leaf-apices.

14. Geniostoma rupestre J. R. & G. Forst. Char. Gen. 24. *t. 12*. 1776, Beschr. Gatt. Pfl. *t. II, f. 12*. 1779; Willd. Sp. Pl. 1: 998. 1797; Spreng. Pl. Min. Cog. 1: 18. 1813, Syst. Veg. 1: 588. 1825; Endl. Gen. Pl. 576. 1838; DC. Prodr. 9: 26. 1845; Benth. in Journ. Linn. Soc. Bot. 1: 97. 1857; F. v. Muell. Contr. Phytog. New Hebr. 13. 1873; Gilg & Benedict in Bot. Jahrb. 56: 542. 1921; Guillaumin in Bull. Soc. Bot. Fr. 72: 701. 1927, in op. cit. 76: 299. 1929, in Journ. Arnold Arb. 13: 22. 1932, in Journ. Linn. Soc. Bot. 51: 557. 1938.

PLATE 1, FIGURE 14

Geniostoma "densiflora" sensu Guillaumin in Bull. Mus. Hist. Nat. [Paris] II. 9: 295. 1937, non Baillon (1880).

Shrub or small tree to 10 m. high, glabrous throughout except for some floral parts, the branchlets slender, subterete or somewhat compressed-quadrangular, 1–2 mm. in diameter distally; stipules intrapetiolar, forming a subtruncate or obtusely deltoid sheath 1–1.5 mm. high; leaves glabrous, petiolate, the petioles slender, 5–10 mm. long, the blades thin-chartaceous to subcoriaceous, ovate to elliptic-ovate,

often rather narrowly so, 3–14 cm. long, 1–4 cm. broad, acute and decurrent or rarely somewhat rounded at base, acuminate or obviously cuspidate at apex, entire, the costa sulcate above, raised beneath, the lateral nerves 5–9 per side, slightly raised on both surfaces, the veinlets plane, mostly obscure; inflorescences axillary among the leaves, dichasial, 5–15-flowered, glabrous, the peduncle short, flattened, 1–2 mm. long, bibracteate at apex, the bracts lanceolate, to 1.5 mm. long, the axes slender, 2–5 mm. long, bibracteate at nodes, the pedicels 2–5 mm. long, slightly flared and bracteolate below calyx; flowers externally glabrous, borne in triflorous (or irregular) dichasia; calyx cupuliform, the lobes deltoid-ovate, 0.7–1 mm. long, 3-nerved; corolla 2.5–3 mm. long, short-tubular, slightly urceolate, with reflexed (?) lobes, divided to middle, the tube glabrous within at base, sparsely pilose above and around throat with white reflexed trichomes 0.5–0.8 mm. long, these also on filaments, the lobes glabrous distally within, sparsely pilose with similar trichomes toward extreme base along nerves, the venation comparatively complex, each lobe supplied by a central nerve producing a lateral branch on each side near base of tube or sometimes higher, the branches ascending into the lobe and there often with brief lateral branches, occasionally the lobe supplied by two equal (or very rarely by three equal) veins ascending distinct from base of tube; stamens inserted at throat, the filaments deltoid-ligulate, 0.3–0.4 mm. long, pilose, the anthers narrowly oblong-deltoid, about 0.8 mm. long, minutely apiculate at apex, distally or entirely glabrous; ovary glabrous, subglobose, 0.6–0.7 mm. in diameter, the style filiform, glabrous, 0.6–0.7 mm. long, the stigma globose or subglobose, about 0.5 mm. in diameter, capsule 7–10 mm. long, 3–4 mm. broad.

TYPE LOCALITY: Tanna, New Hebrides; type collected by J. R. & G. Forster on Cook's second voyage, cited below.

DISTRIBUTION: Known with certainty from the New Hebrides (several islands) and the Santa Cruz Islands; also reported from New Caledonia, as discussed below. The specimens available to us are noted as shrubs or small trees to 10 m. high; the flowers are said to emit a strong foetid odor that attracts flies. Adequate altitudinal data are not available, but presumably *G. rupestre* is a lowland species.

SANTA CRUZ ISLANDS: VANIKORO: *Kajewski* 650 (A, UC, US).
NEW HEBRIDES: ESPIRITU SANTO: Mt. Tabwemanana, in open grassland, *I. & Z. Baker* (Oxford Univ. Exped.) 29 (BM). AMBRYM: Mt. Touo, *de la Rüe* (2nd Voy.) in 1935–36 (A). ERROMANGA: Wuppenbu (?), *Cheesman* 20 (K). TANNA: *J. R. & G. Forster* 103 (BM type, K); "*Herb. Pallas*" (coll. Forster?) (BM); *W. Anderson* in 1774 (BM). ANEITYUM: Anelgahaut Bay, *Kajewski* 728 (A, Bish, NY, US).

Geniostoma rupestre has been the traditional "catch-all" for Pacific specimens of the genus, even though Gilg & Benedict in 1921 expressed the opinion that it was a local species limited to the New Hebrides. They apparently had access to some portion of the original Forster material from Tanna. At this time we cannot be certain as to the precise identity of the several New Caledonian sheets referred to *G. rupestre* by Guillaumin, but it is quite probable that the range of the species does extend to that island and perhaps also to the Solomons. However, on the basis of existing material we feel assured that it does not occur east of the New Hebrides.

Since *G. rupestre* is the type species of the genus, some importance is attached to the Forster material, fortunately preserved in good condition. The four specimens cited above from Tanna are so similar in all respects that one may believe them to be parts of the same Forster collection. As holotype we designate the British Museum sheet that is clearly labeled as a Forster collection; previously none of these sheets has been so designated.

Among the species with comparatively long corolla-throat trichomes, *G. rupestre* is readily distinguished from its only close allies, for instance *G. samoense* and *G. insulare*, by its glabrous habit and usually acuminate leaf-blades. A closer superficial resemblance exists between *G. rupestre* and the Fijian *G. macgregorii*, but the indument of the corolla in these two species is uniformly and strikingly different, even though this character is not obvious upon superficial examination.

15. Geniostoma insulare Smith & Stone, sp. nov. PLATE 1, FIGURE 15

Frutex vel arbor gracilis ad 5 m. nonnunquam ad 15 m. alta praeter corollae partem interiorem demum glabra, vel innovationibus ramulis petiolis foliorum costa subtus inflorescentiae axibusque arcte puberulis (pilis patentibus rufis circiter 0.1 mm. longis), ramulis juventute saepe quadrangularibus 1–3 mm. crassis demum subteretibus glabrisque; stipulis intrapetiolaribus in vagina 1–1.5 mm. alta rotundata vel obtusa conjunctis; foliis plerumque comparative parvis, petiolis 3–9 (–11) mm. longis complanatis superne subalatis, laminis chartaceis vel subcoriaceis, ovatis vel ellipticis interdum elliptico-obovatis raro obovatis, 2–12 cm. longis, 1–7 cm. latis, vulgo circiter 5×2.5 cm., basi rotundatis subtruncatis obtusis vel late acutis et plus minusve decurrentibus, apice rotundatis vel acutis interdum minute mucronatis vel cuspidatis vel retusis, margine integris, costa supra sulcata subtus elevata, nervis lateralibus supra saepe subdepressis subtus prominulis, venulis subobscuris; inflorescentiis axillaribus dichasialibus 5–15-floris, pedunculo 1–3 mm. longo, axibus pedicellisque 2–5 (–7) mm. longis interdum puberulis, bracteis inconspicuis; calyce cupuliformi, lobis

deltoideo-ovatis circiter 1×1.3 mm. 1–3 (–5)-nervatis; corolla breviter tubulosa 3–3.5 mm. longa fere ad medium lobata, tubo faucibus pilis pallidis retrorsis 0.4–0.8 mm. longis hirtello, lobis deltoideo-ovatis circiter 1.5 mm. longis latisque supra basim glabris, nervatio subintricato, corollae quoque loba nervo unico cum nervis lateralibus 2 plus minusve tubi medio ornato praedita, nervis 3 subparallelibus vel curvatis in lobam adscendentibus et ibi venulas breves laterales paucas gerentibus; staminium filamentis ad 0.2 mm. longis pilosis, antheris deltoideis circiter 0.8 mm. longis apice acutis vel minute mucronulatis; ovario subgloboso 0.7–0.9 mm. diametro, stylo ad 0.6 mm. longo, stigmate subclavato-obovoideo inconspicue bilobato papilloso 0.7–0.9 mm. longo; capsula ellipsoidea vel sphaeroidea, 5–14 mm. longa, 3–5.5 mm. lata, apiculata, seminibus ovoideis circiter 1.2× 0.7 mm. minute papillosis.

The species here described as new appears to be the most abundant *Geniostoma* in Tonga, and in some forms it occurs more sparingly in both Fiji and Samoa. Specimens which we now refer here have been variously identified in herbaria as *G. rupestre*, *G. vitiense*, and *G. calcicola*. Of these species, *G. insulare* is most closely allied to *G. rupestre*, from which it differs in its quite dissimilar foliage, the leaf-blades being most often rounded to obtuse at apex and only occasionally broadly acute or bluntly cuspidate. In general the veins supplying corolla-lobes branch high in the tube rather than near or at the base as is frequent in *G. rupestre*, but this character is not entirely dependable. Our var. *tongense* of the new species, in its closely but harshly puberulent vegetative parts, suggests *G. calcicola*, which we now believe to be represented only by the type collection from Fulanga, Fiji. However, *G. insulare* never has its foliar indument extending to both surfaces of the leaf-blades, this being limited even in var. *tongense* to the ventral costae and a few of the laterals. The complex involving *G. insulare*, *G. rupestre*, and *G. calciola* is not satisfactorily understood from available material and the present solution is admittedly provisional, pending further observation or experiment. Two varieties, one of which has three quite distinct forms, are distinguished as follows:

Vegetative parts glabrous . . . . . **var. insulare**
Leaf-blades elliptic or ovate, rarely somewhat obovate, rounded or merely acute at base and apex, not cuspidate.
Capsules ellipsoid, comparatively narrow; Tonga and Fiji . . . **f. insulare**
Capsules sphaeroid; Fiji . . . . . **f. sphaerococcum**
Leaf-blades mostly obovate, gradually decurrent at base, rounded or broadly acute and cuspidate at apex; Samoa . . . . . **f. cuspidatum**
Vegetative parts (innovations, branchlets, petioles, and usually leaf-blades on ventral costae) puberulent; Tonga and Niue . . . . . **var. tongense**

15a. Geniostoma insulare var. **insulare**

Varietas typica; partibus vegetativis glabris; foliorum laminis plerumque ellipticis vel ovatis raro subobovatis, basi obtusis vel rotundatis interdum subdecurrentibus, apice rotundatis vel obscure mucronatis vel late acutis; capsulis ellipsoideis vel sphaeroideis.

15a (1). Geniostoma insulare var. **insulare** forma **insulare**

Geniostoma rupestre var. *ellipticum* A. Gray in Proc. Amer. Acad. 4: 33, *nomen*. 1859.

Forma typica; foliorum laminis plerumque ellipticis vel ovatis; capsulis ellipsoideis.

Type in the herbarium of the University of California, No. 296979, collected at edge of mangrove swamp near Nukualofa, Tongatabu, Tonga, near sea level, June–August, 1926, by W. A. Setchell & H. E. Parks (No. 15334). Duplicates at Bish, GH, US.

ADDITIONAL SPECIMENS EXAMINED:

TONGA: HA'ABAI GROUP: KAO: *Yuncker* 15900 (US). NOMUKA: Seaside thicket, *Yuncker* 15821 (US). NIUATOPUTAPU: Summit of range east of Vaipoa, *Hürlimann* 366 (US). TAFAHI: Path to the Piu 'o Tafahi, *Hürlimann* 432 (US). TONGATABU GROUP: TONGATABU: Peninsula west of Hofoa, *Hurlimann* 83 (US); Vahe Ha'ake, *Setchell & Parks* 15357 (UC); near Ha'atafu, *Setchell & Parks* 15575 (UC); below Ha'akame village, *Yuncker* 15284 (US); near Niutoua, *Yuncker* 15111 (US); without precise locality, *U.S. Expl. Exped.* (source of the name *G. rupestre* var. *ellipticum*, GH, NY), *Lister* in 1889 (K), *Setchell & Parks* 15231 (UC), 15247 (UC). Tonga, without further locality: *D. Nelson* (BM).

FIJI: VANUA LEVU: Mathuata: Seanggangga Plateau, in drainage of Korovuli River, near Natua, *Smith* 6868 (A, Bish, K, US). Thakaundrove: Maravu, near Salt Lake, *Degener & Ordonez* 14170 (A, Bish, K). FULANGA: Limestone formation on lagoon cliff, *Smith* 1203 (Bish, GH, K, NY, UC, US).

DISTRIBUTION: Tonga and Fiji; the plant is recorded as a low shrub or slender tree not much exceeding 3 m. in height, usually occurring in thickets near sea level or in xerophilous or fog forest upward to 500 m., frequently on limestone; the flowers are white or greenish white.

LOCAL NAMES AND USE: *Te'e pilo a Maui* (recorded by various collectors in Tonga); *faefaelunga* (Niuatoputapu); *mbitimbiti* (Fulanga). Hürlimann indicates that the plant is used in Tongan medicine.

As the nomenclaturally typical form and variety of *G. insulare* we have indicated the population with glabrous habit, prevailingly elliptic or ovate leaf-blades, and ellipsoid capsules.

15a (2). Geniostoma insulare var. **insulare** forma **sphaerococcum** Smith & Stone, f. nov. PLATE 2, FIGURE 20

Forma foliorum laminis ovatis acutis saepe basi rotundatis vel subtruncatis; e forma typica capsulis sphaeroideis distinguitur.

Type in the U.S. National Herbarium, No. 1674613, collected in hills above Namalata and Ngaloa Bays, Kandavu, Fiji, alt. 200–400 m., October 14, 1933, by A. C. Smith (No. 112). Duplicates at Bish, GH, K, NY, UC.

ADDITIONAL SPECIMENS EXAMINED:

FIJI: VITI LEVU: Naitasiri: Woods near Tamavua, *Gillespie* 3610 in part (NY); near road beyond Nasinu, *Gillespie* 3610 in part (Bish, UC). OVALAU: Northwest of Levuka, *Gillespie* 4566 (Bish, NY, UC). KANDAVU: Hills above Namalata and Ngaloa Bays, *Smith* 71 (Bish, GH, K, NY, UC, US); without precise locality, *Tothill* 614 (K). VANUA MBALAVU: Nambavatu, *Tothill* 615 (K). FULANGA: Limestone formation, *Smith* 1142 (Bish, GH, K, NY, UC, US). Fiji, without further locality: *U.S. Expl. Exped.* (US).

DISTRIBUTION: Fiji, known from the several islands mentioned above, where it occurs as a tree 5–15 m. high from sea level up to 400 m. alt., often in rocky formations or on limestone.

LOCAL NAME: *Mboimboinda* (Kandavu, Fulanga).

The cited specimens differ from the typical form of our var. *insulare* primarily in having consistently globose or sphaeroidal capsules; the leaf-blades also tend to be slightly different in shape, being predominantly ovate and rounded or nearly truncate at base. However, the indicated nomenclatural position seems best to show the relationship within *Geniostoma* of this puzzling population, on the basis of available material. In form the capsules suggest those of *G. dictyoneurum*, described above, from which *G. insulare* differs in the free veinlets of its corolla-lobes and in the smaller, more coriaceous, and usually more acute leaf-blades.

15a (3). Geniostoma insulare var. insulare forma **cuspidatum** Smith & Stone, f. nov.

Forma foliorum laminis plerumque obovatis interdum ellipticis apice cuspidatis et capsulis late ellipsoideis e forma typica differt.

Type in the herbarium of the Bernice P. Bishop Museum, collected on the summit of Mt. Fao, Upolu, Samoa, alt. 680 m., September 6, 1929, by Erling Christophersen (No. 569). Duplicate at UC.

ADDITIONAL SPECIMENS EXAMINED:

SAMOA: SAVAII: Near Salaeula, *Christophersen* 2467 (Bish). TAU: Near summit of main range, *Garber* 755 (Bish). Samoa, without further locality: *U.S. Expl. Exped.* (US), *Whitmee* in 1876–77 (GH).

Distribution: Known only from the few scattered cited Samoan collections, at altitudes up to 680 m.; the plants are said to be shrubs or trees up to 5 m. high.

Although the cited Samoan material seems clearly to belong to the typical variety of *G. insulare*, it represents a local variant which, at least for the present, seems worthy of formal recognition.

15b. Geniostoma insulare var. tongense Smith & Stone, var. nov.

Planta e varietate typica partibus vegetativis et inflorescentiae ramulis arcte puberulis distinguitur; ramulis demum glabratis; foliorum laminis ex ovatis ellipticis utroque subacutis interdum subrotundatis; capsulis ellipsoideis.

Type in the herbarium of the University of California, No. 297257, collected on the plateau on Eua, Tonga, in June or July, 1926, by H.E. Parks (No. 16261). Duplicates at Bish, GH, US.

ADDITIONAL SPECIMENS EXAMINED:

TONGA: VAVA'U GROUP: VAVA'U: Coastal cliff above Leimatua, *Yuncker* 16057 (US). TONGATABU GROUP: EUA: Above Honuma, *Yuncker* 15505 (US); above Fuai, *Yuncker* 15379 (US), *Hürlimann* 190 (US); cliffs at Likio, *Parks* 16097 (UC), 16395 (UC); terrace north of Vaingana Creek, *Hürlimann* 275 (US); without precise locality, *Lister* in 1889 (K), *Cartwright* in 1889 (K).

NIUE: Rocks near Alofi, *Yuncker* 10152 (Bish).

DISTRIBUTION: Tonga and Niue; the variety is recorded as a shrub or as a small tree approaching 5 m. in height and with a trunk 5–18 cm. in diameter, occurring in the forests of level places or along limestone cliffs, elevations of sea level up to 240 m. having been indicated; the flowers are white or greenish, with a disagreeable odor.

LOCAL NAME: *Te'e pilo a Maui* has been recorded in Tonga, as for var. *insulare*.

As implied in our discussion of the species as a whole, these conspicuously puberulent individuals from Tonga and Niue comprise a population of *G. insulare* that seems worthy of varietal recognition.

16. Geniostoma biseriale Rechinger in Rep. Sp. Nov. 6: 325. 1909, in Denkschr. Akad. Wiss. Wien 85: 329. *t. 9, f. 2.* 1910; Christophersen in Bishop Mus. Bull. 128: 175. 1935.

PLATE 1, FIGURE 16

Shrub or small tree 2–4 m. high, glabrous throughout except for some floral parts, with slender pale gray-brown subterete or obscurely quadrangular branchlets, these distally about 2 mm. thick; stipules intrapetiolar, forming a short subtruncate sheath 1–1.2 mm. long; leaves subsessile, the petioles at most 2 mm. long, the blades oblong-elliptic or narrower and lanceolate-elliptic (rarely slightly lanceolate-ovate), subauriculate, cordate, or subcordate at base, acuminate at apex, 6–15 cm. long, 2–6 cm. broad, the costa sulcate above, raised beneath, the lateral nerves 7–12 per side, slightly raised on both surfaces, the veinlets obscure; inflorescences axillary among the leaves, dichasial, 5–10-flowered, the peduncle 1–2 mm. long, the axes and pedicels glabrous, 1–3 mm. long, bracteate, the flowers glabrous externally; calyx cupuliform, the lobes 0.8–1 mm. long, deltoid-ovate; corolla short-tubular, 3.5–4.2 mm. long, lobed nearly to middle, the tube glabrous basally within, at throat sparsely pilose with trichomes 0.3–0.4 mm. long, the lobes deltoid-ovate, glabrous distally, the venation complex, that of each lobe derived from a single central main nerve producing 1 or 2 pairs of lateral branches in the tube, these in turn producing 1 or 2 lateral branches, all ascending into the lobe; stamens inserted at throat, the filaments about 0.2 mm. long, the anthers narrowly deltoid-oblong, 0.6–0.8 mm. long; ovary glabrous,

depressed-globose, about 0.7 mm. high and 0.9 mm. broad, the style slender, glabrous, 1.5–2 mm. long, the stigma (in our specimens poorly preserved) apparently obovoid, about 0.7 mm. long; capsule ellipsoid, 7–8 mm. long, 2–4 mm. broad, apiculate.

TYPE LOCALITY: Upolu, Samoa, in forest near Tiavi, at 700 m. alt.; the type is *Rechinger* 446, presumably deposited in the Berlin Herbarium and subsequently destroyed. The cited illustration is excellent and permits adequate understanding of the concept.

DISTRIBUTION: Endemic to Samoa, and thus far known from few collections from Savaii and Upolu, occurring in forest between 400 and 1500 m. alt.; it is said to be a shrub or small tree up to 4 m. high, with white flowers.

SAMOA: SAVAII: Papa'afu, crater-rim, *Christophersen* 2727 (Bish, UC, NY); above Sili, *Christophersen* 3152 (Bish, UC, NY). UPOLU: Ridge above Malololelei, *Christophersen* 11 (Bish, US).

Geniostoma biseriale is readily distinguished from other species of our region by its essentially sessile leaves, of which the petioles do not exceed 2 mm. in length, the blades being proportionately unusually narrow, prevailingly cordate or even subauriculate at base. The indument of the corolla-throat is short, suggesting that the closest relatives of *G. biseriale* may be *G. gracile* and *G. macgregorii*, but the relationship is not close.

Excluded Species

Geniostoma microphyllum Seem. in Bonplandia 10: 37, nomen. 1862, Fl. Vit. 164. 1866.

FIJI: VITI LEVU: Namosi (?): "Navua River," *Seemann* 304 (BM, GH, K type); Rewa: Summit of Central Road, Suva, *Tothill* 611 (K).

This taxon is not a *Geniostoma*, but appears to be rubiaceous. We judge it to be a juvenile form of a *Psychotria*, probably of a lianoid species, suggestive of *P. serpens* L. The Seemann specimen was mentioned by A. Gray (in Proc. Amer. Acad. 5: 320. 1862), who stated that the specimen, first labeled as a *Gaertnera*, was a new *Geniostoma*. The nature of the stipules, the leaf structure, and the apparent climbing habit (adventitious roots appearing at the nodes of the stem) exclude this plant from *Geniostoma*. We hope to be able to state more precisely the identity of this puzzling plant, but are not prepared to do so at this time.

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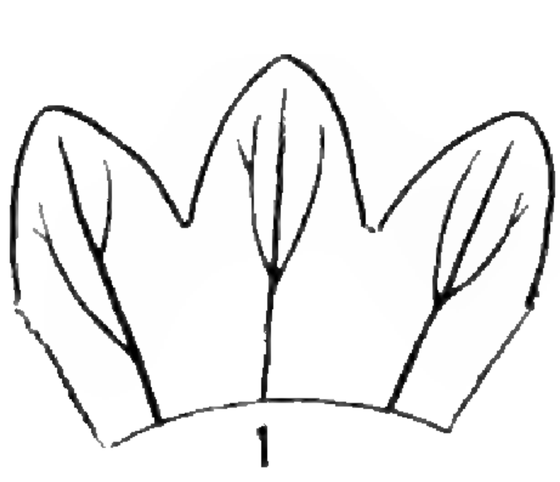
PLATES

PLATE 1

Corolla-lobe venation-patterns in *Geniostoma.* The types of venation of 16 species are shown, all × 5; each figure illustrates 3 lobes and the corresponding part of the corolla-tube. FIGURES 1, *G. macrophyllum;* 2, *G. stipulare;* 3, *G. confertiflorum;* 4, *G. clavigerum;* 5, *G. univervium;* 6, *G. vitiense;* 7, *G. gracile;* 8, *G. macgregorii;* 9, *G. calcicola;* 10, *G. dictyoneurum;* 11, *G. fleischmannii;* 12, *G. stenocarpum;* 13, *G. samoense;* 14, *G. rupestre;* 15, *G insulare;* 16, *G. biseriale.*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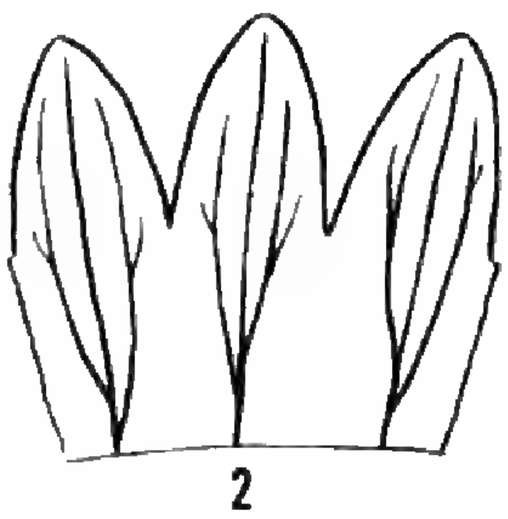
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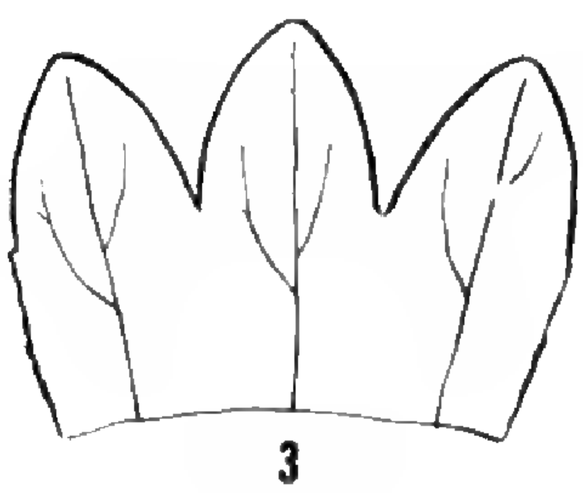
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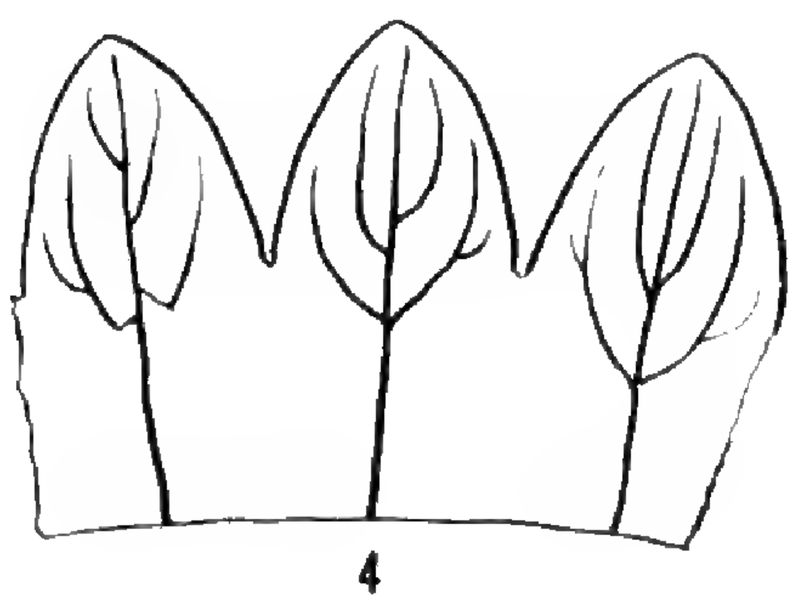
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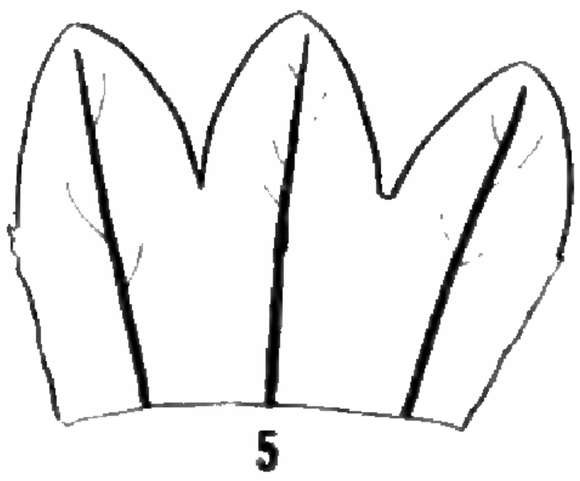
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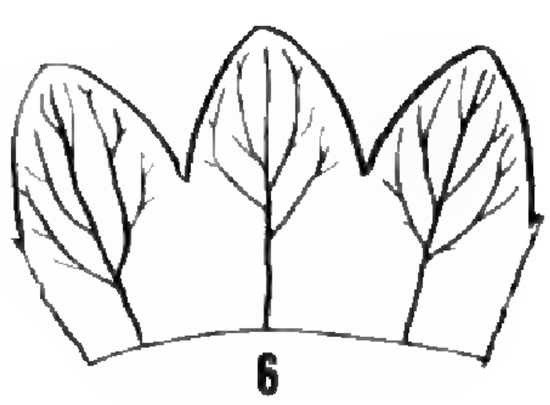
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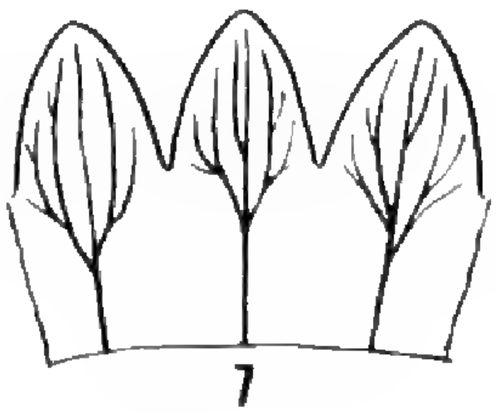
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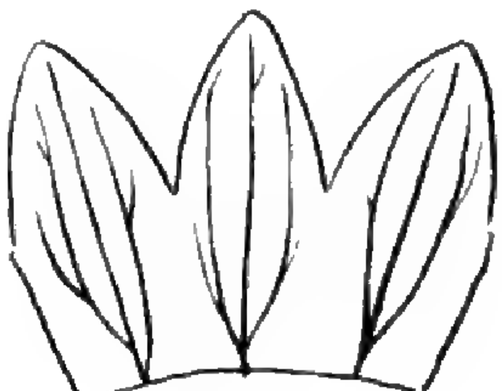
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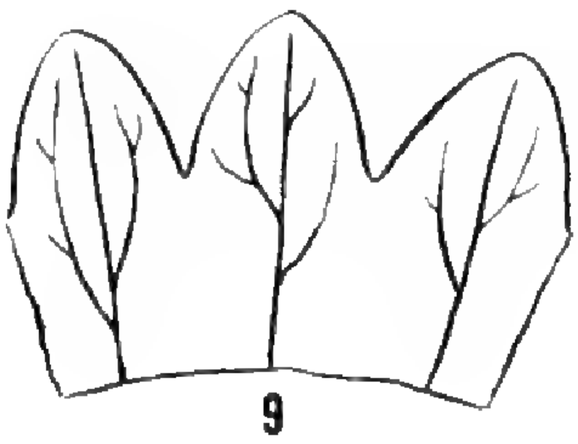
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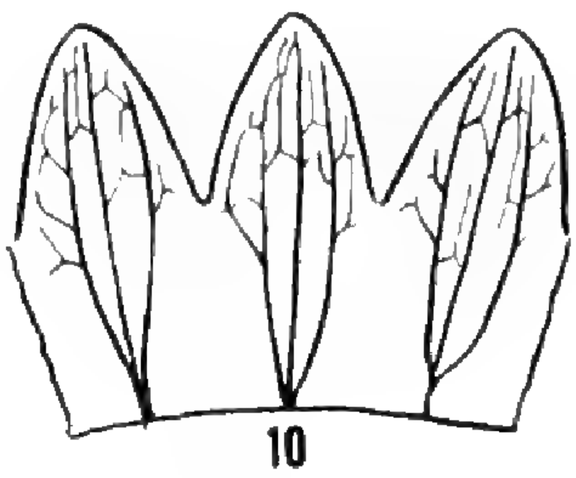
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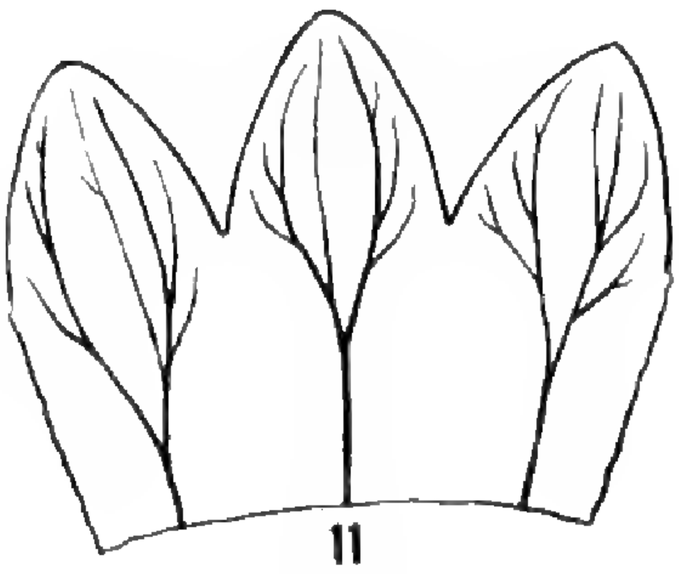
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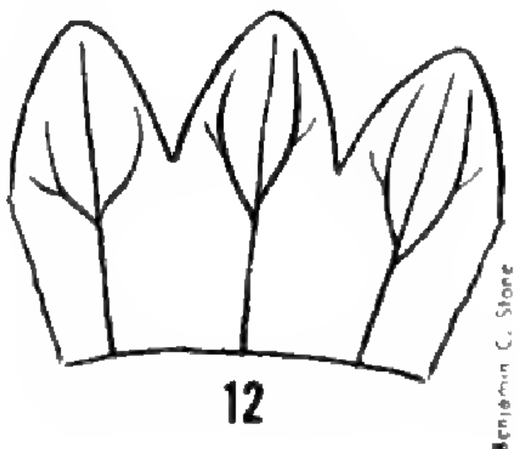
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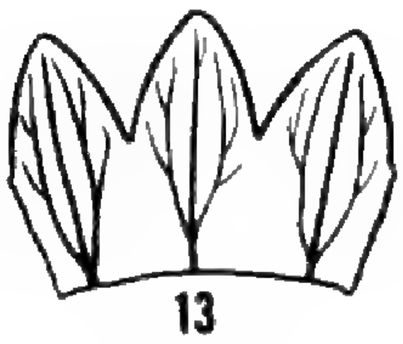
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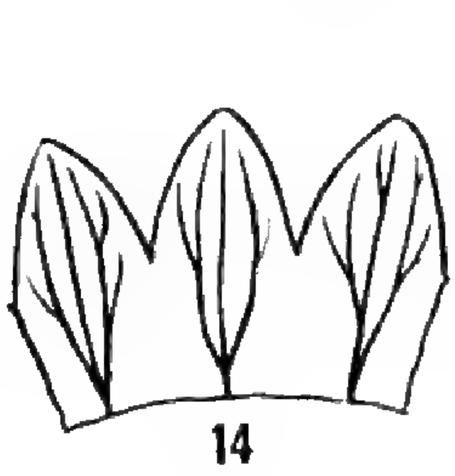
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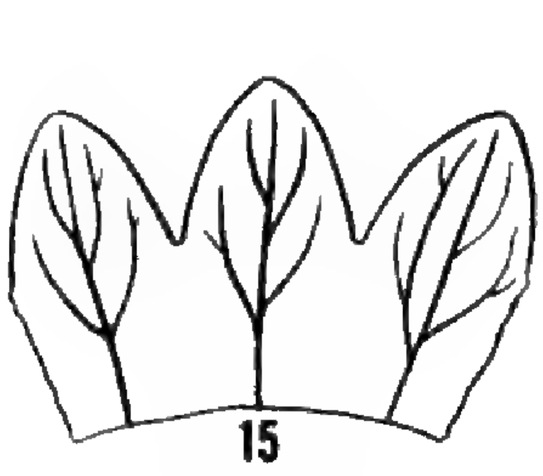
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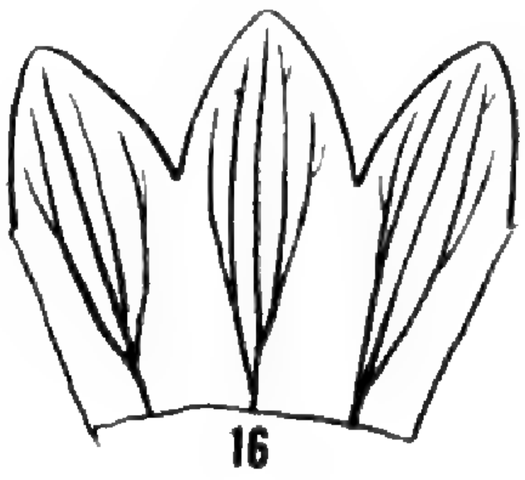
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[For explanation see opposite page.]

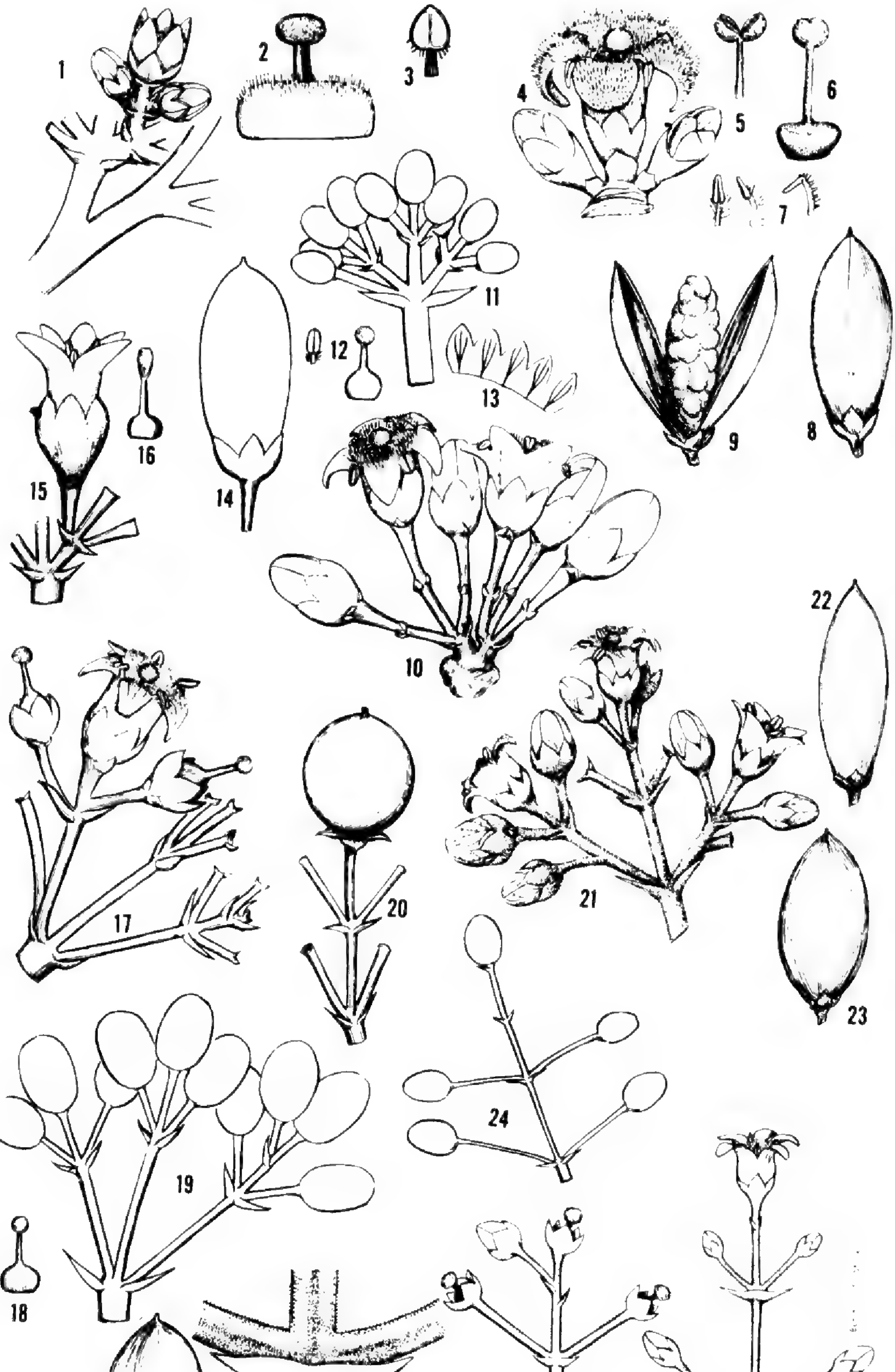
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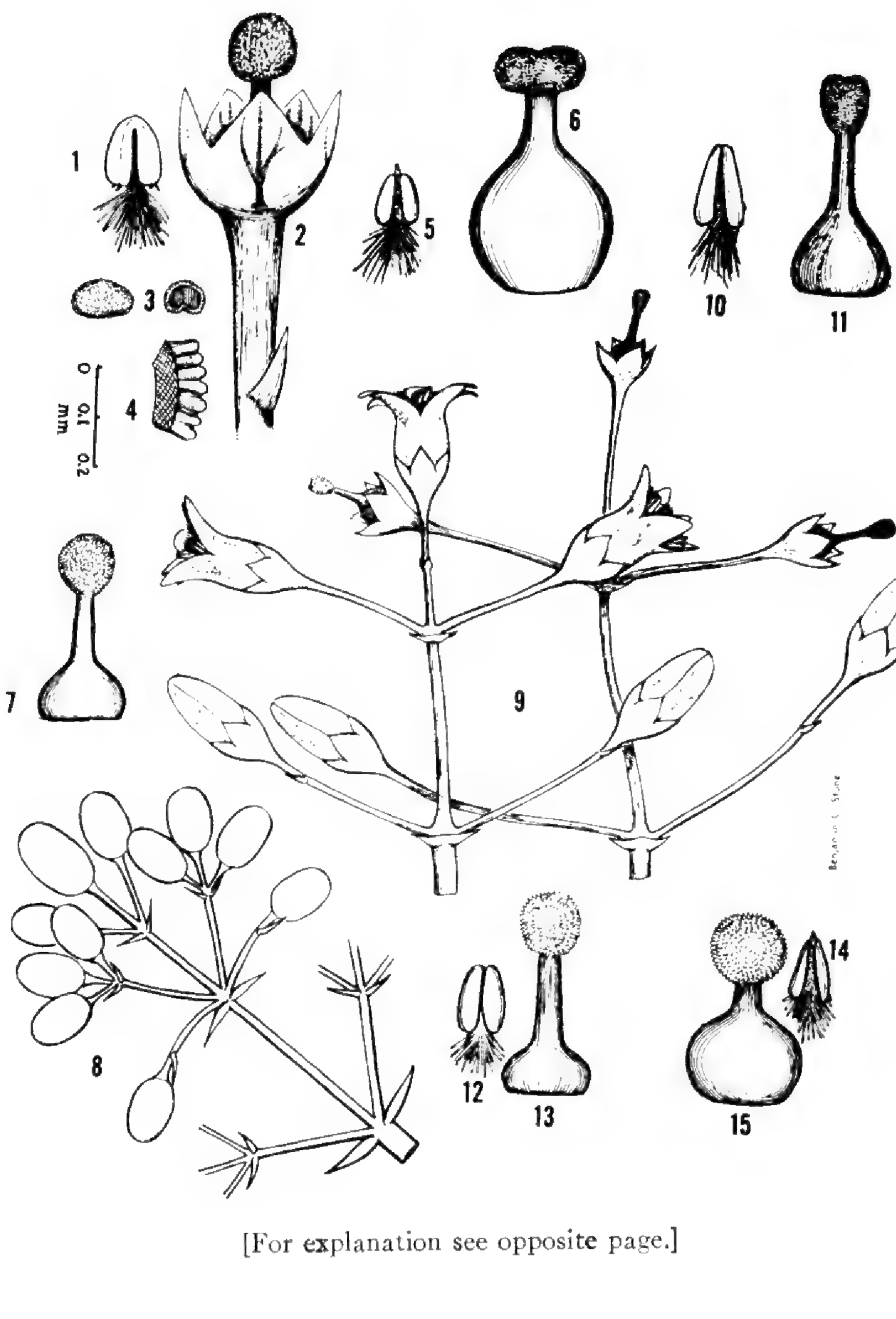
PLATE 2

Floral features of *Geniostoma*. FIGURES 1–3, *G. macrophyllum:* 1, portion of inflorescence, × 2.5; 2, gynoecium, × 10; 3, stamen, × 10. FIGURES 4–9, *G. stipulare:* 4, ultimate dichasium, × 5; 5, stigma, showing lobes, × 5; 6, gynoecium, × 5; 7, stamens, × 5; 8, capsule before dehiscence, × 2.5; 9, capsule after dehiscence, × 2.5. FIGURES 10–14, *G. uninervium:* 10, inflorescence with flowers, × 5; 11, schematic diagram of young inflorescence, × 5; 12, stamen and gynoecium, × 2.5; 13, calyx, showing venation, × 2.5; 14, capsule in outline, × 2.5. FIGURES 15, 16, *G. confertiflorum:* 15, portion of inflorescence with flower, × 2.5; 16, gynoecium, × 2.5. FIGURES 17–19, *G. macgregorii:* 17, part of inflorescence with flower and gynoecia, × 2.5; 18, gynoecium, × 2.5; 19, schematic diagram of inflorescence, × 2.5. FIGURE 20, *G. insulare* f. *sphaerococcum:* capsule and part of inflorescence, × 2.5. FIGURES 21–23, *G. vitiense:* 21, inflorescence, × 2.5; 22, 23, capsules, × 2.5. FIGURE 24, *G. calcicola:* schematic diagram of inflorescence, × 2.5. FIGURE 25, *G. samoense* var. *samoense:* inflorescence and flowers, × 2.5. FIGURE 26, *G. samoense* var. *parviflorum:* inflorescence and flowers, × 2.5. FIGURES 27, 28, *G. samoense* var. *samoense:* 27, greatly enlarged view of inflorescence-node with bract; 28, capsule, × 2.5.

PLATE 3

Floral features of *Geniostoma*. FIGURES 1–4, *G. samoense* var. *samoense:* 1, stamen, × 5; 2, flower past anthesis, with pedicel, × 5; 3, seed in side view and cross-section, × 10; 4, portion of wall of seed in cross-section, × 50. FIGURES 5, 6, *G. samoense* var. *parviflorum:* 5, stamen, × 5; 6, gynoecium, × 5. FIGURES 7, 8, *G. stenocarpum:* 7, gynoecium, × 5; 8, schematic diagram of inflorescence, × 2.5. FIGURES 9–11, *G. gracile:* 9, two inflorescences, one with flowers at anthesis, the other slightly later, × 2.5; 10, stamen, × 5; 11, gynoecium, × 5. FIGURES 12–15, *G. vitiense:* 12, 13, stamen and gynoecium from "long-styled" or hermaphrodite flower, × 5; 14, 15, stamen and gynoecium from "short-styled" or pistillate flower, × 5.



[For explanation see opposite page.]

UNITED STATES NATIONAL MUSEUM

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VOLUME 37, PART 1

STUDIES OF PACIFIC ISLAND PLANTS, XVII
THE GENUS GENIOSTOMA (LOGANIACEAE) IN THE NEW HEBRIDES, FIJI, SAMOA, AND TONGA

By ALBERT C. SMITH and
BENJAMIN C. STONE

SMITHSONIAN INSTITUTION • WASHINGTON, D.C. • 1967

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UNITED STATES NATIONAL MUSEUM

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VOLUME 37, PART 2

MOSSES OF THE EASTERN HIGHLANDS, NEW GUINEA, FROM THE 6th ARCHBOLD EXPEDITION, 1959

By EDWIN B. BARTRAM

BULLETIN OF THE UNITED STATES NATIONAL MUSEUM

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MOSSES OF THE EASTERN HIGHLANDS, NEW GUINEA, FROM THE 6th ARCHBOLD EXPEDITION, 1959

By Edwin B. Bartram [1]

The moss collections, represented by 375–400 numbers, made by L. J. Brass, H. M. van Deusen, and J. D. Collins in the Eastern Highlands of northeastern New Guinea have been acquired by the Smithsonian Institution. These were entrusted to me for determination. They are a welcome and important supplement to the collection made by Ross G. Robbins in the Western Highlands. The results bring into sharp focus a number of significant aspects of the New Guinea moss flora.

As a result of active field work by Mr. Brass and Mr. Robbins this insular moss flora has been expanded in recent years to about 850 species. This is a large number for an area the size of New Guinea and it emphasizes the astonishing richness of this tropical flora. Every new collection adds new records and new species to a total which may eventually reach or exceed 1,000 species. The rugged terrain of the interior, with some peaks reaching altitudes of 14,000 to 16,500 ft., provides a wide variety of habitats which increase the interest and complexity of the flora. While far from complete, our present knowledge is broad enough to form the basis for some general conclusions. The percentage of endemism is abnormally high. Between 350 and 400 species, or nearly half of the known flora, have been described as new from New Guinea. Critical studies may reduce the figure to some extent, but the ratio of endemic species is likely to remain disproportionally high. Of the remaining 400 to 500 species by far the greater part is broadly representative of the Indo-Malayan areas to the west from where the bulk of the present flora has been derived. A limited number of species are common to the New Zealand-Australian area, but the affiliation in this direction is rather limited. A few species from the alpine crests of the higher peaks such as *Calliergon sarmentosum*, *Calliergon wilhelmense* (near

[1] Edwin B. Bartram, 1878–1964. Shortly before his death the author transferred his personal herbarium to the Farlow Herbarium at Harvard University where he had long been honorary curator of mosses.

C. turgescens), and *Meesea triquetra* show such disjunct geographical distribution as to preclude any logical explanation. If the North Pole was located in the south central Pacific ages ago, as has been suggested, these relicts may represent waifs of circumpolar distribution that have survived in sanctuary niches, but this is of course only a random guess. The implications are too complex and extensive for my modest attainments. The fact remains that the New Guinea moss flora is predominantly Malaysian in character and probably represents the southeastern front of a broad pattern of geographical distribution extending east to Fiji and Samoa.

In the following list, species not previously recorded from New Guinea are preceded by an asterisk. A complete series of specimens is deposited in the herbarium of the United States National Museum, Washington, D.C., and in the Farlow Herbarium at Harvard University.

Andreaeaceae

Andreaea rupestris Hedw.

Mt. Wilhelm, east slopes: on stones on alpine grassland, 13,500 ft., *Van Deusen* 29896; cushioned in crevices near summit, 14,500–14,700 ft., *Collins* 29958, 29959; cushioned on a rock near summit, 14,700 ft., *Van Deusen & Collins* 30027.

Andreaea (Enervia) novo-guinensis Bartr. sp. nov.

Robusta, caespitosa, caespitibus densis, fuscescentibus, nitidiusculis. Caulis 5–7 cm. altus, parce ramosus, ramis obtusis. Folia erecta, imbricata, late ovata, profunde concava, obtusa, 1.5–2.5 mm. longa, 1.2 mm. lata, ecostata; marginibus integris, erectis, superne inflexis; cellulis superioribus parvis, rotundatis, incrassatis, laevissimis, diam. 5–6 μ, basilaribus internis linearibus, incrassatis, porosis, externis parvis, rotundatis. Folia perichaetialia parva caulina similia; theca in pseudopodio crasso, ovalis folia perichaetialia vix superans.

Type in the U.S. National Herbarium, collected on moist ground near summit, at 14,700 ft. altitude, east slopes, Mt. Wilhelm, New Guinea, June 18, 1959, by Van Deusen and Collins (no. 30029).

This remarkable species in an unusual habitat is characterized by the robust habit, the turgid stems, and the broad, concave, bluntly pointed leaves.

Fissidentaceae

Fissidens filicinus D. & M.

Kassam: wet, shady bank of a small stream in *Castanopsis*-oak forest, 1370 m., 32414.

Ditrichaceae

Ditrichum sericeum Bartr.

Mt. Wilhelm, east slopes, 14,700 ft.: on ground near summit, *Collins* 29964; in a moist crevice near summit, *Van Deusen & Collins* 30032.

Dicranaceae

Trematodon longicollis Mx.
Mt. Otto, south slopes, 7,300 ft., 29122.

Campylopodium euphorocladum (C. M.) Besch.
Purosa, Okapa area: terrestrial on roadside in rain forest, 1950 m., 31610.

Dicranella setifera (Mitt.) Jaeg.
Arau: on a clay roadbank in forest, 1400 m., 32069.

Campylopus (Eucampylopus) crispifolius Bartr. sp. nov.

Dense caespitosus, caespitibus fuscescentibus. Caulis brevis, vix 1 cm. longus, dense foliosus; folia sicca arcte flexuosa vel crispata, humida erecto-patentia, e basi oblonga sensim acuminata, 4 mm. longa, 0.5 mm. lata; marginibus erectis, integris, apice solum denticulatis; costa inferne 375 μ lata; cellulis basilaribus hyalinis, parietibus teneris, rectangularibus, 12–18 μ latis, superioribus parvis, rhomboideis; alaribus nullis. Caetera ignota.

Type in the U.S. National Herbarium, collected on a seepage slope in alpine grassland, at 3560 m. elevation, east slopes, Mt. Wilhelm, New Guinea, June 14, 1959, by L. J. Brass (no. 29894).

The absence of alar cells suggests some affinity with *C. robbinsii* Bartr., but the flexuose-crispate leaves less slenderly acuminate are quite distinctive.

Campylopus (Palinocraspis) wilhelmensis Bartr. sp. nov.

Caespitosus, caespitibus lutescentibus intus fuscescentibus. Caulis erectus, 4–5 cm. altus, simplex vel sparse ramosus, rubro-tomentosus. Folia sicca erecta, humida flexuoso-patentia, e basi breviter oblonga sensim subulato-acuminata, 5 mm. longa, ad 0.7 mm. lata; marginibus erectis, inferne integris, superne remote et minute denticulatis; costa inferne 300 μ lata; cellulis basilaribus breviter oblongis, 14–18 μ latis, parietibus firmis, marginalibus e seriebus 4–5 abrupte angustioribus, alaribus distinctis, fuscis vel hyalinis, sat auriculatis; superioribus parvis, subquadratis. Caetera ignota.

Type in the U.S. National Herbarium, collected on a tree stump in moist forest, at 2740 m. elevation, east slopes, Mt. Wilhelm, New Guinea, July 1, 1959, by L. J. Brass (no. 30237).

The costal structure is similar to that of *C. morobensis* Bartr., but the stems are evenly foliate, tomentose and the leaves shorter.

Campylopus comosus Bosch & Lac. (?)
Sterile. Morobe District, Botanic Gardens, Lae: on tree-fern stem supports of epiphytic orchids, 200 ft., 29111.

Campylopus caudatus (C. M.) Mont.
Mt. Wilhelm, east slopes: on deadwood on alpine grassland, 3560 m., 29891.

Campylopus (Palinocraspis) atro-fuscescens Bartr. sp. nov.

Dense caespitosus, caespitibus inferne nigricentibus superne lutescentibus. Caulis erectus, dense foliosus. Folia erecta, flexuosa, humida erecto-patentia, e basi ovata sensim subulato-acuminata, 6 mm. longa, 0.6 mm. lata; marginibus erectis, integris, apice solum parcissime denticulatis; costa breviter excurrente, inferne circa 0.3 mm. lata; cellulis superioribus parvis, rotundatis, basilaribus linearibus, porosis margines versus angustioribus, alaribus subquadratis, vix distinctis, fugacissimis. Caetera ignota.

Type in the U.S. National Herbarium, forming cushions on alpine grassland, at 13,100 ft. elevation, east slopes, Mt. Wilhelm, New Guinea, June 15, 1959, by J. D. Collins (no. 29941).

Suggestive of *C. clemensiae* Bartr. in some respects but distinct in the darker color, the evenly foliate stems, and the differentiated alar cells which while present are not well defined.

Campylopus exasperatus Brid.

Mt. Wilhelm, east slopes: on wet ground in alpine grassland, 13,100 ft., *Collins* 29939.

Campylopus archboldii Bartr.

Mt. Wilhelm, east slopes: on exposed rock in alpine grassland, 3560 m., 29821a; on rocks of a shady stream in forest, 2770 m., 30450.

Campylopus umbellatus (Arn.) Par.

Morobe District, Wau-Edie Creek road: 5,800 ft., 29162. Kaindi: on clayey moist roadbank, 2060 m., 29548. Mt. Wilhelm, east slopes: on alpine grassland, 13,100 ft., 29942, 30090a. Mt. Otto: on rocks of a creek bank in forest, 2200 m., 30839. Mt. Michael, northeast slopes: on exposed rock in forest, 2000 m., 31533.

Atractylocarpus dicranoides Dix.

Mt. Wilhelm, east slopes: on deadwood in subalpine forest, 3560 m., 30045.

***Amphidium cyathicarpum** (Mont.) Broth.

Mt. Wilhelm, east slopes: on dry ground under a rock overhang on alpine grassland, probably fertilized by owl pellets and droppings, 3650 m., *Van Deusen* 30151.

Distribution: Guatemala, western South America, Australia, New Zealand, Africa.

***Symblepharis reinwardtii** (D. & M.) Bosch & Lac.

Mt. Michael: on rocks of summit, 3650 m., *Brass & Collins* 31259.

Distribution: Sikkim, Burma, Java, Borneo, Philippine Islands.

Dicranoweisia macrocarpa Bartr.

Mt. Wilhelm, east slopes: cushioned high on a tree in forest, 2770 m., 30470.

Holomitrium stenobasis Dix.

Mt. Wilhelm, east slopes: on a tree in edge of subalpine forest, 3700 m., 30119.

Holomitrium austro-alpinum Bartr.

Mt. Otto: on alpine grassland of the summit, 3540 m., 31038.

Cryptodicranum armittii (C. M.) Bartr.

Arau: on tree trunks, 1400 m., 31960a, 31961.

Dicranoloma perarmatum Broth.

Morobe District, Mt. Kaindi: on decayed wood in forest, 7,200 ft., 29165; on edge of a path in *Castanopsis* forest, 2000 m., 29526. Mt. Wilhelm, east slopes: on tree trunk in subalpine forest, 3650 m., 29868.

Dicranoloma laevifolium (Broth. & Geh.) Par.

Mt. Wilhelm, east slopes: in small cushions on tree trunks in subalpine forest, 3650 m., 29869; on wet ground in long-grass community of alpine grassland, 3800 m., 30121.

Dicranoloma dicarpum Hornsch.

Mt. Michael, northeast slopes: on lower trunks of big trees in *Castanopsis-Nothofagus* forest, 2000 m., 31504. Purosa, Okapa area: on leaf littered ground in *Castanopsis* forest, 2050 m., 31844.

Dicranoloma braunii (C. M.) Par.

Mt. Wilhelm, east slopes: on tree trunks in forest, 2740 m., 30234. Purosa, Okapa area: on undergrowth in rain forest, 1950 m., 31667; on tree trunks in *Castanopsis* forest, 2050 m., 31843. Arau: on tree in *Castanopsis* forest, 1400 m., 31976.

Dicranoloma blumii (Nees) Par.

Mt. Michael: on trees in subalpine forest, 3500 m., *Brass & Collins* 31318.

Braunfelsia enervis (D. & M.) Par.

Mt. Wilhelm, east slopes: on a tree in moist, mossy forest, 2600 m., 30490.

Leucobryaceae

***Leucobryum chlorophyllosum** C. M.

Morobe District, Oomsis: on buttress roots of a great *Anisoptera* tree, 200 m., 29268a.

Distribution: Ceylon, Java, Philippine Islands, Celebes, Sumbawa, Timor.

Leucobryum sanctum Hpe.

Purosa, Okapa area: on tree trunks in rain forest, 1950 m., 31693. Kassam: on logs and bases of trees in *Castanopsis*-oak forest, 1370 m., 32433.

Leucobryum candidum (Brid.) H. f. & W.

Mt. Otto, south slopes, 2000 m.: low on trees in *Castanopsis* forest, 31111.

Leucobryum pentastichum D. & M.

Morobe District, Oomsis: on buttress roots of a great *Anisoptera* tree, 200 m., 29266, 29267a.

Octoblepharum albidum Hedw.

Morobe District: Botanic Gardens, Lae: on tree-fern stem supports of epiphytic orchids, 29105.

Leucophanes glaucescens C. M.

Morobe District, Umi River, Markham Valley: low on a tree in rain forest, 480 m., 32584; Botanic Gardens, Lae: on tree-fern stem supports of orchids, 200 ft., 29107b.

Leucophanes octoblepharioides Brid. var. **korthelsii** (D. & M.) Fleisch.

Morobe District, Botanic Gardens, Lae: 200 ft., 29106a.

Calymperaceae

Syrrhopodon ciliatus (Hook.) Schwaegr.

Morobe District, Botanic Gardens, Lae: on tree-fern stem supports of epiphytic orchids, 200 ft., 29107.

***Syrrhopodon philippinensis** Bartr.

Morobe District, Oomsis: on buttress roots of a great *Anisoptera* tree, 200 m., 29268.

Distribution: Philippine Islands.

Calymperes hyophylaceum C. M.

Morobe District, Botanic Gardens, Lae: on tree-fern stem supports of epiphytic orchids, 200 ft., 29109.

Calymperes moluccense Schwaegr.

Morobe District, Botanic Gardens, Lae: on tree-fern supports of epiphytic orchids, 29107a, 29110.

Calymperes tahitense (Sull.) Mitt.

Morobe District, Kelly Bros. place on Bulolo Road, about 3 miles west of Lae: ca. 20 m., between buttress roots of tree, 29104a.

Pottiaceae

Hyophila involuta (Hook.) Jaeg.

Mt. Michael, northeast slopes: on rocks in *Castanopsis-Nothofagus* forest, 2000 m., 31535, 31537a, 31544. Morobe District, Umi River, Markham Valley: on moist rock face in rain forest, 480 m., 32627.

Trichostomum angustatum (Mitt.) Fleisch.

Mt. Otto, south slopes: underside of a rock overhang, 2200 m., 30923.

Trichostomum subulifolium Bartr.

Mt. Wilhelm, east slopes: on a tree trunk in subalpine forest, 3560 m., 29847. Mt. Michael, northeast slopes: on rock in *Castanopsis-Nothofagus* forest, 2000 m., 31543.

***Leptodontium warnstorfii** Fleisch.

Mt. Wilhelm, east slopes: alpine grassland, 13,500 ft., *Van Deusen* 29895.

Distribution: Java.

***Streptopogon erythrodontus** (Tayl.) Wils.

Mt. Wilhelm, east slopes: tufted on exposed branches of a tree in subalpine forest 3560 m., 30068.

Distribution: Guatemala, Colombia, Ecuador, Peru, Bolivia, Hawaii, Madagascar, Africa.

The occurrence of this species in New Guinea presents a problem in geographical distribution that is hard to explain with any satisfaction. The species is fairly well distributed along the American Cordillera from Bolivia to Guatemala. It is also known from the crater of Haleakala, Maui, Hawaii, and the variety *rutenbergii* (C. M.) Salm. from Madagascar and the African continent. This is the only known record from the southwest Pacific area. The species appears to be of austral origin and has fanned up through South America and Africa.

Grimmiaceae

Grimmia affinis Hornsch.

Mt. Wilhelm, east slopes: cushioned on rocky slopes, 14,700 ft., *Van Deusen & Collins* 30026.

This species has been recorded from the Himalayas and Ceylon at high altitudes under the name of *G. ovalis* (Hedw.) Lindb., but according to the studies by Dr. Sayre (Bryologist 55:258, 1952), Hornschuch's name will take precedence. Here the setae are distinctly curved when dry but strictly erect when moist.

Rhacomitrium crispulum (H. f. & W.) H. f. & W.

Mt. Wilhelm, east slopes: exposed rock in alpine grassland, 3650 m., 29874; in crevices near summit, 14,500–14,700 ft., J. D. Collins 29961, 29962; on a rock in alpine grassland, 3560 m., 30086, 30091; terrestrial in alpine grassland, 3800 m., 30122; on rocks of a shady stream in forest, 2770 m., 30448.

Rhacomitrium lanuginosum (Hedw.) Brid. var. **pruinosum** H. f. & W.

Mt. Wilhelm, east slopes: alpine grassland, 13,100 ft., *Collins* 29940; 3700 m., *Brass* 29996.

Funariaceae

Entosthodon subulatus Bartr.

Mt. Wilhelm, east slopes: on wet ground in alpine grassland, 13,100 ft., *Collins* 29938.

Entosthodon contortus Bartr.

Mt. Michael: wet ground edging small pools on alpine grassland, 3560 m., 31432 bis.

Funaria hygrometrica Hedw.

Morobe District, Mt. Kaindi: roadbank, 2200 m., 29593. Mt. Wilhelm, east slopes: burnt ground, 2770 m., 30673. Purosa, Okapa area: burnt ground, 31841.

Splachnaceae

Tayloria octoblepharis (Hook.) Mitt.

Mt. Wilhelm, east slopes: terrestrial in an open place in long-grass community of alpine grassland, 3850 m., 30118; on log, 2740 m., 30241a.

Bryaceae

Mielichhoferia (Eumielichhoferia) novo-guinensis Bartr. sp. nov.

Paroica: caespitosa, caespitibus densis, superne pallide viridibus, inferne fuscescentibus, nitidiusculis. Caulis erectus, usque ad 2 cm. altus, inferne denudatus, dein dense foliosus. Folia imbricata, ovato-lanceolata, tenuiter acuminata, 2 mm. longa, 0.45 mm. lata; marginibus erectis, superne minute denticulatis; costa inferne 0.75 μ lata, valde excurrente; cellulis anguste linearibus, infimis brevioribus. Seta 2 cm. longa; theca erecta vel leniter inclinata, oblongo-cylindrica, deoperculata ad 4 mm. longa; operculum obtuse conicum; endostomium hyalinum, laevissimum, corona basilaris ad 50 μ alta, processus anguste lineari, 375 μ longi, medio c 17 μ lati; spori ferruginei, papillosi, diam. 20 μ.

Type in the U.S. National Herbarium, collected in a crevice near summit, at 14,500–14,700 feet elevation, east slopes, Mt. Wilhelm, New Guinea, June 16, 1959, by J. D. Collins (no. 29966).

This species resembles *M. javanica* Broth. in some respects, but the larger, finely acuminated leaves 2 mm. long with the costa excurrent in a short arista are good diagnostic characters.

Pohlia elongata Hedw.

Mt. Wilhelm, east slopes: on base of tree in edge of subalpine forest, 3650 m., 29866.

***Pohlia flexuosa** Hook.

Morobe District, Wau-Edie Creek road: on moist, clayey roadbank, 5,800 ft., 29159.

Distribution: Apparently widely distributed in tropical regions. Himalayas, West Indies, Central & South America.

Brachymenium nepalense Hook.

Mt. Wilhelm, east slopes: on tree trunk in forest, 2740 m., 30231.

***Anomobryum cymbifolium** (Lindb.) Broth.

Mt. Wilhelm, east slopes: on rocks in an alpine grassland stream, 3560 m., 30089.

Distribution: Himalayas, Khasia, South India, Java, Amboina, Philippine Islands.

Bryum argenteum Hedw.

Morobe District, Mt. Kaindi: open ground, 2250 m., 29680. Mt. Wilhelm, east slopes: on a stump in alpine grassland, 3560 m., 30085; on open ground in alpine grassland, 4080 m., 30172; on bare ground in forest 2600 m., 30718.

Bryum porphyroneuron C. M.

Morobe District, Botanic Gardens, Lae: limestone of a rockery, 200 ft., 29114; Kaindi: on wet rock, 29551; on log, 29552; Gurakor: on log in forest, 640 m., 29414. Mt. Wilhelm, east slopes: open flood banks of Pengagl Creek, 2770 m., 30269.

***Bryum australe** Hampe.

Morobe District, Kaindi: roadbank in forest, 2060 m., 29681.

Distribution: Australia.

Bryum nitens Hook.

Morobe District: Umi River, Markham Valley, 480 m., 32627a.

Bryum (Doliolidium) wilhelmense Bartr. sp. nov.

Gracile, dense caespitosum, caespitibus pallide fuscescentibus, intus dense intertextis. Caulis ad 5 cm. altus, ramosus. Folia erecta, imbricata; folia caulina ovata breviter aristata, ad 0.8 mm. longa, comalia longiora; marginibus integris, erectis; costa breviter excurrente; cellulis superioribus rhomboideis, 35–40 μ longis, 10 μ latis, basilaribus infimis subquadratis. Seta gracilis ad 2.5 cm. longa; theca horizontalis, deoperculata 2 mm. longa.

Type in the U.S. National Herbarium, collected on exposed rock in alpine grassland, at 3560 m. elevation, east slopes, Mt. Wilhelm, New Guinea, June 11, 1959, by L. J. Brass (no. 29821). Paratype at same locality, on rocks in a stream in alpine grassland, *Brass* 30093.

In some respects this species resembles *B. junghuhnianum* Hpe. of Java, but the elongated stems and shorter-pointed longer leaves are quite distinctive.

Bryum novo-guinense Bartr.

Mt. Wilhelm, east slopes: on rocks in an alpine grassland stream, 3560 m., 30090b.

Bryum truncorum Brid.

Mt. Wilhelm, east slopes: on a tree in subalpine forest, 3560 m., 30150; on a tree stump in forest, 2740 m., 30233; lower trunk of tree in mossy forest, 2770 m., 30349. Mt. Otto, south slopes: on a log in forest, 2480 m., 30902.

Bryum crassulum Bartr.

Morobe District, Kaindi: on a log in forest, 2150 m., 29703.

Rhodobryum giganteum (Hook.) Schp.

Mt. Wilhelm, east slopes: terrestrial in moist forest, 2900 m., 30388.

Leptostomaceae

Leptostomum intermedium Broth.

Mt. Wilhelm, east slopes: on tree in subalpine forest, 3560 m., 29892. Mt. Otto, south slopes: on dead small tree in forest, 2480 m., 30903.

Mniaceae

Orthomniopsis elimbata Noguchi.

Morobe District, Wau-Edie Creek road: 5,800 ft., on moist, rocky roadbanks, 29161. Mt. Wilhelm, east slopes: on thick terminal branches of a *Ternstroemia* tree in forest, 2770 m., 30352.

As no. 30352 is in good fruit, the sporophyte of this species may be described. Dr. Noguchi was correct in assuming that this species was an *Orthomniopsis*. *Mnium rotundifolium* Bartr., which is exactly the same thing, will therefore be reduced to synonymy.

Perichaetial leaves spatulate, rounded, unbordered, 7–8 mm. long. Seta solitary or two from one perichaetium, 5 mm. long, 0.5 mm. thick, slightly curved; capsule nodding, oblong-cylindric, abruptly contracted to the seta, 4 mm. long, 2 mm. thick; peristome double, teeth brown, papillose, linear-lanceolate, 0.8 mm. long, endostome papillose, pale, basal membrane about half the height of the teeth, segments about equaling the teeth. Operculum, calyptra, and spores not seen.

Rhizogoniaceae

Hymenodon parvulus Bartr.

Mt. Wilhelm, east slopes: on trees in forest, 2770 m., 30348, 30351.

No. 30348 contains many fruiting plants. The sporophyte may be

described as follows: Perichaetium small, leaves about 1 mm. long, broadly ovate, laxly areolate, unbordered, costa excurrent. Seta 12 mm. long, pale brown; capsule erect, relatively large, oblong-cylindric, urn 2.5 mm. long, operculum conic-rostrate, 1 mm. long, oblique; outer peristome lacking, endostome pale, segments 0.3 mm. long from a rather high basal membrane projecting about 50 μ above the rim; spores pale, smooth, diameter 10 μ; calyptra cucullate, small, barely covering the operculum.

Rhizogonium spiniforme (Hedw.) Bruch.

Morobe District, Oomsis: on buttress roots of a great *Anisoptera* tree, 200 m., 29267; Gurakor: base of tree, 640 m., 29505. Arau: on tree roots, 1400 m., 31926. Kassam: on tree trunks and rotting wood, 1370 m., 32339.

Hypnodendraceae

Hypnodendron diversifolium Broth.

Purosa, Okapa area: on logs in rain forest, 1950 m., 31697. Arau: on surface roots in oak-*Castanopsis* forest, 1400 m., 31926a.

Hypnodendron auricomum Broth. & Geh.

Morobe District, Kaindi: on stem of a dead tree fern in forest, 2060 m., 29789. Mt. Wilhelm, east slopes: terrestrial in deep shade in subalpine forest, 3560 m., 29849. Mt. Otto, south slopes: terrestrial on edge of a stream in *Castanopsis* forest, 2000 m., 31112.

Hypnodendron (Euhypnodendron) brassii Bartr. sp. nov.

Robustum, pallide viride, nitidum. Caulis usque ad 10 cm. altus, erectus, rigidus, alte stipitatus, dense rufo-tomentosus, stipite foliis pallidis, adpressis, acuminatis, superne dense ramosus, ramis bipinnatis, ca. 3 cm. longis, densissime congestis; folia ramea complanata, ovato-lanceolata, breviter acuminata; marginibus erectis, superne grosse et irregulariter serratis; costa tenuis, infra apicem folii evanida, dorso superne serrata; cellulis linearibus, basilaribus infimis laxioribus. Setae numerosi, ad 10, rubri, 2.5 cm. longi; theca cum collo cylindrica, valde plicata, 5 mm. longa.

Type in the U.S. National Herbarium, collected on ground in *Castanopsis*-oak forest, at 1400 m. elevation, Arau, New Guinea, Oct. 12, 1959, by L. J. Brass (no. 32042).

This unusual and attractive species is immediately distinguished by the tomentose stipes and the branches densely crowded in a compact, globular head up to 6 cm. in diameter, suggestive in a way of *H. junghuhnii* but much denser and more pronounced.

Mniodendron humile Lindb.

Mt. Wilhelm, east slopes: on dead tree in forest 2740 m., 30243; on a log in forest, 2770 m., 30451. Mt. Otto, south slopes: terrestrial in stunted forest, 3300 m., 31039. Arau: on logs in forest, 1400 m., 31978.

Bartramiaceae

***Conostomum australe** Sw.

Mt. Wilhelm, east slopes: on moist ground near summit, 14,700 ft., *Van Deusen & Collins* 30030.

Distribution: Colombia to Fuegia, Falkland Islands, Auckland Islands, Campbell Islands, Australia, New Zealand.

Bartramia sp.

The leaves up to 4 mm. long differ from those of either *B. cubica* Dix. or *B. conica* Bartr. where they are 7–8 mm. long. In the absence of fruit it seems unwise to propose a new species.

Mt. Wilhelm, east slopes: cushioned in crevices near summit, 14,500–14,700 ft., *Collins* 29963.

Philonotis secunda (D. & M.) Bosch & Lac.

Mt. Wilhelm, east slopes: wet, boggy ground in long-grass community in alpine grassland, 3560 m., 30070; on rocks in stream, 2770 m., 30450a. Mt. Otto, south slopes: wet stream bank, 2200 m., 30841. Morobe District, Umi River, Markham Valley: 480 m., 32529.

Philonotis novoguinensis Reim.?

Mt. Wilhelm, east slopes: in shallow seepage water on open flood terraces of Pengagl Creek, 2770 m., 30407.

The broader leaf cells (to 10 μ wide) suggest that these plants may be referred to Reimer's species, but in the absence of fruit the determination is questionable.

Breutelia romeri Fleisch.

Mt. Wilhelm, east slopes: on moist ground in long-grass community of alpine grassland, 3560–3850 m., 29819, 30117.

Spridentaceae

Spiridens reinwardtii Nees.

Mt. Wilhelm, east slopes: on stem of a tree fern in subalpine forest, 3560 m., 30149.

Spiridens aristifolius Mitt.

Purosa, Okapa area: in rain forest, forming large clumps often on stems of tree ferns, 1950 m., 31682.

Spiridens perichaetialis Bartr. & Willis.

Morobe District, Wau-Edie Creek road: on dead tree fern, 1850 m., 29777. Mt. Wilhelm, east slopes: on trees, 2770 m., 30292. Mt. Otto, south slopes: on small trees in forest, numerous plants radiating from their supports, 2480 m., 30892. Mt. Michael: on trees in forest, 3100–3290 m., *Brass & Collins* 31302. Purosa, Okapa area: on stems of tree ferns, 1950 m., 31682a.

Orthotrichaceae

Zygodon reinwardtii Al. Br.

Mt. Wilhelm, east slopes: on deadwood in subalpine forest, 3560 m., 29820.

Zygodon intermedius B. & S.

Mt. Wilhelm, east slopes: under a rock overhang in alpine grassland, 3650 m., *Van Deusen* 30152.

Ulota anguste-limbata Bartr.

Mt. Wilhelm, east slopes: on upper branches of trees in subalpine forest, 3650 m., 29867; on dead branch in edge of subalpine forest, 3900 m., 30120.

Ulota splendida Bartr.

Mt. Wilhelm, east slopes: in golden yellow masses on alpine grassland, 13,100 ft., *Collins* 29944; alpine grassland, 13,100 ft., *Collins* 29945a.

Desmotheca apiculata (D. & M.) Lindb.

Morobe District, Botanic Gardens, Lae: 200 ft., on roots of epiphytic orchid, 29108; Oomsis: matted high on a dipterocarp tree in forest, 150 m., 29194; Umi River, Markham Valley, 480 m., on tree trunk, 32617.

Macromitrium erubescens Bartr.

Morobe District, Kaindi: high epiphyte in *Nothofagus* forest, 2150 m., 29701. Mt. Otto, south slopes: high epiphyte in *Castanopsis* forest, 2000 m., 31116.

Macromitrium orthostichum Nees.

Mt. Otto, south slopes: on tree, 2000 m., 31117a.

Macromitrium (Goniostoma) brevirameum Bartr. sp. nov.

Humile, fuscescens. Caulis prostratus, ramosus, rami breves, 4–5 mm. alti, cuspidati. Folia sicca spiraliter contorta, humida patula, anguste oblongo-lanceolata, obtusa, apiculata, 1.5 mm. longa, 0.3 mm. lata; marginibus integris, superne sinuatis; costa percurrente; cellulis superioribus parvis, papillosis, sat incrassatis, basilaribus linearibus, grosse tuberculosis. Seta gracilis, 5–7 mm. longa; theca elliptica, microstoma, ore angulato; calyptra glabra, basi integra.

Type in the U.S. National Herbarium, collected as a high epiphyte in *Castanopsis* forest, at 2000 m. elevation, south slopes, Mt. Otto, New Guinea, Aug. 17, 1959, by L. J. Brass (no. 31117). Paratype on a living branch in forest undergrowth, at 2000 m. elevation, northeast slopes, Mt. Michael, *Brass* 31485.

This species has much in common with *M. speirophyllum* Bartr., but the distinctions are sharply defined. Here the branches are less than 5 mm. high, the leaves only 1.5 mm. long, the upper leaf cells 7–8 μ in diameter and minutely papillose and the color brownish green, while in *M. speirophyllum* the branches are about 1 cm. long, the leaves 2–2.5 mm. long, the upper cells 12–15 μ in diameter and highly papillose and the color deep, rich red.

Macromitrium novo-guinense Bartr.

Mt. Wilhelm, east slopes: on bark of a dead tree in forest, 2750 m., 30229; on tree trunks in subalpine forest, 3560 m., 29823.

Macromitrium sublongicaule Bartr.

Mt. Wilhelm, east slopes: on high branches of a tree in forest, 2770 m., 30353. Mt. Otto, south slopes: high epiphyte in *Castanopsis* forest, 2000 m., 31118, 31117b. Arau: on tree trunks in *Castanopsis* forest, 1400 m., 31943, 31977. Morobe District, Umi River, Markham Valley: on tree trunk, 480 m., 32615.

Macromitrium semipellucidum D. & M.

Morobe District: Kelly Bros. place about 3 miles west of Lae, on Bulolo road, 20 m., 29102; Botanic Gardens, Lae, 200 ft., on tree-fern stem support of an epiphytic orchid, 29112; Umi River, Markham Valley, on a dead stick, 480 m., 32548; on a tree trunk, 32614.

Macromitrium angustifolium D. & M.

Mt. Wilhelm, east slopes: on dead branch, 2740 m., 30230; on tree trunk in forest edge, 2600 m., 30789. Mt. Otto, south slopes: on tree trunk in *Castanopsis* forest, 2000 m., 31113. Kassam: on tree trunk, 1370 m., 32376. Purosa, Okapa area: on a big tree in rain forest, 1950 m., 31796. Morobe District, Kaindi: open, rocky bank of stream in forest, 2060 m., 29549; Umi River, Markham Valley, tree trunk, 480 m., 32616.

Schlotheimia emarginato-pilosa Herz.

Arau: high on trees in *Castanopsis*-oak forest, 1400 m., 31941.

Schlotheimia pilicalyx Broth. & Geh.

Mt. Wilhelm, east slopes: tree trunks in subalpine forest, 3650 m., 29873, 29993. Mt. Otto, south slopes: on alpine grassland of summit, 3540 m., *Brass & Collins* 31038a.

Schlotheimia macgregorii Broth. & Geh.

Mt. Michael: on a tree in forest, 2700 m., 31450. Morobe District, Kaindi: high epiphyte in *Nothofagus* forest, 2150 m., 29702.

Rhacopilaceae

Powellia involuta Mitt.

Mt. Michael, northeast slopes: on stem of small *Pandanus* in *Castanopsis-Nothofagus* forest, 2000 m., 31547. Arau: trunk of *Pandanus* in *Castanopsis*-oak forest, 1400 m., 31942; on stem of *Pandanus* tree, 1400 m., 32039.

Rhacopilum spectabile R. & H.

Purosa, Okapa area: on rotting logs, 1950 m., 31651. Kassam Gap: on log, 1460 m., 32297. Mt. Michael, northeast slopes: on twigs and branches, 2000 m., 31540, 31542, 31549. Mt. Otto, south slopes: on tree in forest, 2200 m., 30840. Morobe District, Wau-Edie Creek road: on log, 5,800 ft., 29163; Mt. Kaindi: on log, 2200 m., 29594 in part.

Hedwigiaceae

Rhacocarpus humboldtii (Hook.) Lindb.

Mt. Wilhelm, east slopes: cushioned on moist ground near summit, 14,700 ft., *Van Deusen & Collins* 30031.

Rhacocarpus alpinus (Wright) Par.

Mt. Wilhelm, east slopes: terrestrial on alpine grassland, 3700 m., 29995.

These plants correspond in all particulars with those from Mt. Kinabalu, Borneo, and also with the scrap from Mt. Wilhelmina (Bartram, E. B., Lloydia 5:275, 1942). The leaves show no trace of a hair-point and are constantly short apiculate. By contrast the plants in no. 30031 all show hair-pointed leaves. I have therefore referred this latter collection to *R. humboldtii* and this one to *R. alpinus* pending a critical revision of the genus.

Cyrtopodaceae

Bescherellea cyrtopus F. v. Muell.

On lower trunks of trees in *Castanopsis* forest, Kassam, 1370 m., 32281.

***Bescherellea elegantissima** Duby.

Mt. Wilhelm, east slopes: low on trees in moist forest, 2740 m., 30245; on tree trunks in forest, 2900 m., 30387; low on trees in open, swampy forest, 2770 m., 30468.

Distribution: New Caledonia, Aneityum.

Ptychomniaceae

Hampeella pallens (Lac.) Fleisch.

Morobe District, Kaindi: on dead branch in forest, 2060 m., 29663.

Prionodontaceae

Neolindbergia brassii Bartr.

Mt. Wilhelm, east slopes: masses low on tree in forest, 2770 m., 30620.

By good fortune these plants are well fruited with the capsules very young and immature, ripe and in prime condition, or old and empty. The sporophyte characters are as follows: perichaetium small, inner leaves erect, 3 mm. long, ligulate from an ovate base, serrulate near apex, costa ending below the acute apex, upper cells small, round, basal cells linear toward costa, small and round in 5–6 rows at margins. Seta 5 mm. long, erect, papillose; capsule globose, brown, glossy, 1 mm. in diam.; operculum oblique, conic-rostrate, 1 mm. long; calyptra cucullate, short, pilose, 2 mm. long; peristome teeth about 0.3 mm. long, linear, hyaline, smooth, inserted below rim; endostome none or fragmentary and rudimentary without segments or cilia; spores 16–20 μ in diam., minutely papillose, exothecial cells irregularly hexagonal, incrassate, smaller and colored in several rows around mouth, annulus none.

Pterobryaceae

Trachyloma indicum Mitt.

Mt. Wilhelm, east slopes: low on trees in subalpine forest, 3560 m., 30069.

Trachyloma tahitense Besch.

Mt. Wilhelm, east slopes: low on trees in moist, mossy forest, 2900 m., 30390.

Endotrichella apiculata Bartr. sp. nov.

Sat robusta, pallide viridis, nitida. Caulis secundarius usque ad 4 cm. longus, simplex, haud complanatus, cum foliis 7 mm. latus. Folia late patentia, rotundato-ovata, ca. 3 mm. longa, 2.2 mm. lata, apice rotundata, apiculata, plicata; marginibus superne minute denticulatis; costa duplex, brevis; cellulis lineari-rhomboideis, incrassatis, infimis fuscis, alaribus nullis. Folia perichaetialia parva, erecta, acuta; seta 1 mm. longa; theca erecta, exserta, oblonga deoperculata 2 mm. longa.

Type in the U.S. National Herbarium, collected on undergrowth in forest, at 1400 m. elevation, Arau, New Guinea, Oct. 6, 1959, by L. J. Brass (no. 31909).

Paratype: On undergrowth in *Castanopsis*-oak forest, 1370 m., Kassam, New Guinea, *Brass* 32439a.

The short, apiculate leaves are distinctive as compared with the other local species.

Endotrichella compressa (Mitt.) Broth.

Arau: on undergrowth in forest, 1400 m., 31910; high on trees in *Castanopsis*-oak forest, 1400 m., 31925. Kassam: tufted on underbrush, 1370 m., 32437.

Endotrichella falcifolia Bartr. sp. nov.

Robusta, superne pallide viridis inferne fuscescens. Caulis secundarius ad 5–6 cm. longus. Folia vix conferta, falcato-secunda, oblongo-lanceolata, filiformiter acuminata, plures plicata, ecostata, 6–7 mm. longa, 1.5 mm. lata; marginibus superne grosse serratis; cellulis superioribus anguste linearibus, incrassatis, basilaribus latioribus, infimis fuscis, alaribus paucis, irregularis. Caetera ignota.

Type in the U.S. National Herbarium, collected on undergrowth in rain forest, at 2000 m. elevation, Purosa, Okapa area, New Guinea, Oct. 1, 1959, by L. J. Brass (no. 31840).

The falcate-secund leaves will separate this species from *E. perplicata* Broth. to which it seems to have some affinity.

Endotrichella elegans (D. & M.) Fleisch.

Morobe District, Gurakor: on branchlets of small tree in a moist ravine in rain forest, 640 m., 29419.

Endotrichella perplicata Broth.

Purosa, Okapa area: on branches of woody undergrowth in rain forest, 1900 m., 31766a. Kassam: on undergrowth in *Castanopsis*-oak forest, 1370 m., 32436.

Endotrichella novae-hannoverae C. M.

Mt. Wilhelm, east slopes: low on tree in moist forest, 2770 m., 30284.

Garovaglia mirabilis Dix.

Kassam: on underbrush in *Castanopsis*-oak forest, 1370 m., 32438. Mt. Michael, northeast slopes: on a rock in *Castanopsis-Nothofagus* forest, 2000 m., 31546. Morobe District, Mt. Kaindi: on dead branchlets in forest undergrowth, 7,200 ft., 29166.

Garovaglia brevifolia Bartr. sp. nov.

Gracilis, fuscescens, nitida. Caulis secundarius usque ad 5 cm. longus, simplex, sat dense foliosus, cum foliis ca. 2 mm. latus. Folia late patentia, apice incurva, late ovata, abrupte apiculata, 2–2.5 mm. longa, 1.3–1.6 mm. lata, leniter plicata, ecostata; marginibus planis, superne denticulatis; cellulis anguste rhomboideis, c. 12 μ latis, 36–48 μ longis, incrassatis, alaribus sat numerosis, oblongis. Perichaetium majusculum, alte convolutum, foliis abrupte breviter acuminatis, marginibus superne denticulatis; theca immersa, oblongo-cylindrica, deoperculata 2 mm. longa, subsessilis.

Type in the U.S. National Herbarium, collected on undergrowth in a semiswampy place in *Castanopsis*-oak forest, at 1370 m. elevation, Kassam, New Guinea, Nov. 5, 1959, by L. J. Brass (no. 32439).

The short, abruptly apiculate leaves and more slender habit are thoroughly distinctive characters in comparison with *G. densifolia* Thw. & Mitt.

Garovaglia papuana Dix.

Mt. Wilhelm, east slopes: low on trees in moist forest, 2740 m., 30246.

Meteoriaceae

Meteorium miquelianum (C. M.) Fleisch.

Mt. Wilhelm, east slopes: on twigs in subalpine forest, 3560 m., 29846; on woody undergrowth in moist forest, 2770 m., 30368. Morobe District, Umi River, Markham Valley: on tree in rain forest, 480 m., 32585.

Floribundaria floribunda (D. & M.) Fleisch.

Arau: on leaf of a Zingiberaceous herb, 1400 m., 32185. Kassam: on woody undergrowth, 1370 m., 32279. Morobe District, Umi River, Markham Valley: on trees, underbrush and leaves in rain forest, 480 m., 32550, 32551.

Floribundaria aurea (Griff.) Broth.

Mt. Wilhelm, east slopes: pendant from underbrush in moist, mossy forest, 2770 m., 30409.

Meteoriopsis reclinata (C. M.) Fleisch.

Morobe District, Gurakor: on leaves, rotten wood and branchlets, 640 m., 29417, 29420a, 29423.

Lembophyllaceae

Camptochaete subporotrichoides (Broth. & Geh.) Broth.

Mt. Wilhelm, east slopes: low on trees in forest, 2900 m., 30391.

Phyllogoniaceae

Orthorrhynchium elegans (H. f. & W.) Reh'dt.

Kassam: on lower trunk of tree in *Castanopsis*-oak forest, 1370 m., 32377.

Neckeraceae

Calyptothecium crispulum (Lac.) Broth.

Mt. Otto, south slopes: on a tree on forest edge, 7,300 ft., 29124.

Calyptothecium extensum Fleisch.

Morobe District, Umi River, Markham Valley: 480 m., 32587.

Calyptothecium urvilleanum (C.M.) Broth.

Kassam: on stilt roots of Pandanus, 1370 m., 32413. Morobe District: Umi River, Markham Valley, 480 m., on trees in rain forest, 32586.

Neckeropsis gracilenta (Lac.) Fleisch.

Morobe District, Gurakor: on leaves and trees in moist rain forest, 640 m., 29420, in part, 29421.

Neckeropsis lepineana (Mont.) Fleisch.

Purosa, Okapa area: on tree trunk, 1900 m., 31767. Arau: on tree trunks, 1400 m., 31907. Kassam: on tree trunks, 1370 m., 32334. Morobe District: Umi River, Markham Valley, on underbrush in rain forest, 480 m., 32549.

Homaliodendron flabellatum (Sm.) Fleisch.
Kassam: on tree trunks, 1370 m., 32280.

Pinnatella mucronata (Lac.) Fleisch.
Morobe District, Umi River, Markham Valley: on dead branches, 480 m., 32531a.

Nemataceae

Ephemeropsis tjibodensis Goeb.
Mt. Michael, northeast slopes: on twigs and leaves of an undergrowth small tree in *Castanopsis-Nothofagus* forest, 2000 m., 31531 in mixture.

Hookeriaceae

Daltonia angustifolia D. & M.
Mt. Wilhelm, east slopes: on deadwood in subalpine forest, 3560 m., 30044; on twigs in forest undergrowth, 2740–2800 m., 30248, 30472, 30740.

Daltonia angustifolia D. & M. var **revoluta** (Broth.) Bartr.
Mt. Wilhelm, east slopes: on a log in moist forest, 2740 m., 30242.

Daltonia contorta C. M.
Mt. Wilhelm, east slopes: on a log, 2740 m., 30242a.

Daltonia aristifolia R. &. C.
Mt. Wilhelm, east slopes: on deadwood in subalpine forest, 3650 m., 29875.

Distichophyllum brevicuspidatum Bartr.
Mt. Michael, northeast slopes: on twigs and leaves, 2000 m., 31531a.

Actinodontium rhaphidostegum (C.M.) Bosch & Lac.
Arau: on a rotting log, 1400 m., 31980a.

Callicostella papillata (Mont.) Mitt.
Purosa, Okapa area: on rotting wood in rain forest, 1950 m., 31696.

Chaetomitriopsis glaucocarpa (Reinw.) Fleisch.
Purosa, Okapa area: on branches of an undergrowth tree in rain forest, capsules a pale, glaucous blue 1950 m., 31797. Kassam: low on woody undergrowth in forest, 1370 m., 32278.

Chaetomitrium nano-hystrix C. M.
Morobe District, Gurakor: on living twigs in rain forest undergrowth, 640 m., 29424.

Chaetomitrium papillifolium Bosch & Lac.
Morobe District, Umi River, Markham Valley; on dead branches and bark in rain forest, 480 m., 32531, 32583.

Chaetomitrium papuanum Bartr.
Arau: on twigs of undergrowth trees, 1400 m., 31929. Kassam: on branches of woody undergrowth, 1370 m., 32435.

Chaetomitrium crispifolium Bartr.
Mt. Wilhelm, east slopes: on a tree trunk, 3560 m., 29850a; on a log in moist forest, 2740 m., 30241.

Chaetomitrium integrifolium Bartr.
Arau: on leaf of an undergrowth tree in *Castanopsis*-oak forest, 1400 m., 31928.

Chaetomitrium pseudopapillifolium Bartr.
Morobe District, Oomsis: on bark and branchlets in rain forest, 100 m., 29243, 29244, 29292, 29293; Umi River, Markham Valley: on a tree trunk, 480 m., 32656.

Thuidiaceae

Pelekium velatum Mitt.

Morobe District, Oomsis: logs in rain forest, 100 m., 29210, 29211; Umi River, Markham Valley, on a log, 480 m., 32613.

Thuidium furfurosum (H. f. & W.) Jaeg.

Morobe District, Oomsis: on rocks on bank of stream in rain forest, 100 m., 29230.

Thuidium investe (Mitt.) Jaeg.

Morobe District, Kaindi: on bark and rotting wood in forest, 2060 m., 29550, 29555.

Thuidium cymbifolium (D. & M.) Bosch & Lac.

Mt. Michael, northeast slopes: on trees and rocks in *Castanopsis-Nothofagus* forest, 31539, 31536. Kassam: on rocks, 1370 m., 32349, 32434, in part.

Amblystegiaceae

***Calliergon sarmentosum** (Wahlenb.) Kindb.

Mt. Wilhelm, east slopes: on wet ground in alpine grassland, 13,100 ft., *Collins* 29943a.

The occurrence of this widely distributed species in the alpine region of New Guinea is noteworthy and significant. It is evidently a waif from the south where it occurs sparingly in New Zealand.

Distribution: Europe, Asia, Fuegia, South Georgia, New Zealand, East Africa.

Calliergon wilhelmense Bartr. sp. nov.

Dense caespitosum, caespitibus fuscescentibus, nitidis. Caules prostrati, parce ramosi, valde tumidi. Folia laxe imbricata, oblongo-ovata, breviter acuminata, profunde concava, usque ad 2 mm. longa, 0.8 mm. lata; marginibus erectis, integris superne inflexis; costa duplex, brevissima; cellulis superioribus, anguste linearibus, 4–5 μ latis, 40–50 μ longis, basilaribus longioribus, incrassatis alaribus sat numerosis, irregulariter quadratis, incrassatis. Caetera ignota.

Mt. Wilhelm, east slopes: forming loose cushions on wet ground on alpine grassland, 13,100 ft., *J. D. Collins* 29943. June 15, 1959.

This species in appearance and detail shows a very close affinity to *C. turgescens* (Th. Jens.) Kindb., but the uniformly short, double costa and the narrower lamina cells seem to be distinguishing characters.

Brachytheciaceae

Pleuropus luzonensis Broth.

Mt. Wilhelm, east slopes: low on a dead tree in forest, 2740 m., 30240; on bark of a big *Podocarpus papuanus* tree, 2770 m., 30469.

Brachythecium plumosum (Hedw.) B. S. & G

Mt. Wilhelm, east slopes: on rocks of a stream in forest, 2600–2800 m., 30447, 30449, 30600, 30738, 30739.

Brachythecium integerrimum Bartr.

Mt. Wilhelm, east slopes: on rocks in an alpine grassland stream, 3560 m., 30090.

Eurhynchium celebicum (Bosch & Lac.) Bartr.

Arau: on a bracket fungus in *Castanopsis*-oak forest, 1400 m., 32194 in mixture.

Rhynchostegiella stellata Bartr.

Morobe District, Kaindi: on a tree in forest, 2060 m., 29554, with hepatics.

Entodontaceae

Erythrodontium julaceum (Hook.) Par.

Morobe District. Wau: in front of District Office on a tree, 3,500 ft., 29156; Umi River, Markham Valley, on a tree in rain forest, 480 m., 32657.

Campylodontium flavescens (Hook.) Bosch & Lac.

Arau: on rotting wood in *Castanopsis*-oak forest, 1400 m., 32062.

Sematophyllaceae

Clastobryella cuculligera (Lac.) Fleisch.

Mt. Wilhelm, east slopes: on branch in forest undergrowth, 2770 m., 30471.

Acanthocladium clarkii Dix.

Mt. Wilhelm, east slopes: pendant from twigs in subalpine forest, 3700 m., 29990.

Acanthocladium gracile Bartr.

Mt. Wilhelm, east slopes: on a tree trunk in subalpine forest, 3560 m., 29850. Morobe District, Kaindi: on moist, clayey roadbanks, 2060 m., 29615.

The falcate-secund leaves suggest that this species may be an *Ectropothecium*. The inflated alar cells of the stem leaves are hard to demonstrate and seem to be large hyaline cells confined to the extreme basal angles as in other species of *Ectropothecium*.

Trismegistia panduriformis (C. H. Wright) Broth.

Purosa, Okapa area: on surface roots in rain forest, 1950 m., 31666.

Trismegistia rigida (H. & R.) Broth.

Arau: on a log in *Castanopsis*-oak forest, 1400 m., 32196.

***Meiothecium attenuatum** Broth.

Morobe District, Wau: on a tree trunk in front of District Office, 3,500 ft., 29157.

Distribution: Philippine Islands.

Meiothecium longisetum Bartr.

Mt. Wilhelm, east slopes: on deadwood in moist, mossy forest, 2900 m., 30389.

Meiothecium microcarpum (Harv.) Mitt.

Morobe District, Botanic Gardens, Lae: 200 ft., on bark of frangipani tree, 29115; Lae: 10 m., on bark of garden Hibiscus tree, 29116.

Brotherella falcata (D. & M.) Fleisch.

Arau: on a rotting log in *Castanopsis*-oak forest, 1400 m., 31979.

Sematophyllum subhumile (C. M.) Fleisch.

Morobe District, Oomsis: tree trunk in rain forest, 200 m., 29265.

Acroporium diminutum (Brid.) Fleisch.
Kassam: on tree trunks, 1370 m., 32432.

Acroporium sigmatodontium (D. & M.) Fleisch.
Arau: on a tree trunk, 1400 m., 31960.

Acroporium secundum (R. & H.) Fleisch.
Purosa, Okapa area: on trees, 1950 m., 31734.

Warburgiella subleptorrhynchoides Fleisch.
Mt. Wilhelm, east slopes: log in forest, 2740 m., 30239, 30249, 30250; on trees in subalpine forest, 3560–3650 m., 29848, 29871, 29893. Mt. Otto: on trees and rotting wood, 2000 m., 31114, 31115. Mt. Michael, northeast slopes: on rotting wood and a bracket fungus, 2000 m., 31550, 31391. Purosa, Okapa area: on rotting logs, 1950 m., 31647, 31649. Arau: on rotting wood, 1400 m., 31940a. Kassam: on a rotting log, 1370 m., 32336. Morobe District, Mt. Kaindi: on deadwood, 2060–2200 m., 29642, 29764.

Trichosteleum laevi-hamatum Dix.
Arau: on rotting wood, 1400 m., 32197.

Trichostelcum novae-guineae Bartr.
Arau: on rotting wood, 1400 m., 31940.

Acanthorrhynchium papillatum (Harv.) Fleisch.
Kassam: on tree trunks, 1370 m., 32337.

Taxithelium nepalense (Schwaegr.) Broth.
Morobe District, Oomsis: on deadwood in rain forest, 150 m., 29193, 29212.

Taxithelium kerrianum (Broth.) Fleisch.
Morobe District, Umi River, Markham Valley: on dead branches, 480 m., 32531b.

Taxithelium isocladum (Lac.) R. & C.
Arau: on leaves of a ground fern, 1400 m., 31975. Morobe District, Gurakor: on leaves of undergrowth shrub, 640 m., 29481.

Glossadelphus zollingeri (C. M.) Fleisch.
Morobe District, Gurakor: on a rock in a stream bed in rain forest, 640 m., 29413.

Glossadelphus prostratus (D. & M.) Fleisch.
Mt. Wilhelm, east slopes: on moist granitic rocks of a stream in forest, 2600 m., 30601.

These plants are less slender than the plants from Mt. Dayman with leaves up to 1 mm. long and 0.45 mm. wide. It is apparently a robust form.

Macrohymenium mitratum (D. & M.) Fleisch.
Arau: on a tree, 1400 m., 31976a.

Macrohymenium novo-guineense Reim.
Mt. Wilhelm, east slopes: on deadwood in edge of subalpine forest, 3700 m., 29994; on exposed trunk of tree in forest, 3150 m., 30705; exposed trunk of tree in subalpine forest, 3600 m., 30148.

These collections differ from *M. mitratum* in the more robust habit, ruddy color, and longer setae. Here as in the material from Mt.

Wilhelmina and Mt. Hagen the setae are from 12–17 mm. long and weakly scabrous above. The leaves vary from 2–2.4 mm. long and from 0.4–0.7 mm. wide. While the leaves are slightly larger than originally described, the robust habit, coloring, and long setae indicate that they should be referred here.

Hypnaceae

Ectropothecium ichnotocladum (C. M.) Jaeg.

Mt. Michael, northeast slopes: on dead bark, 2000 m., 31548. Arau: on deadwood, 1400 m., 31980, 32195. Morobe District, Umi River, Markham Valley: on log, 32530, in part.

Ectropothecium percomplanatum Broth.

Mt. Michael, northeast slopes: on wet rocks in stream, 2000 m., 31534.

Ectropothecium falciforme (D. & M.) Jaeg.

Mt. Wilhelm, east slopes: among tall grasses in alpine grassland, 3560 m., 29822; on a rotting log, 2740 m., 30235. Mt. Michael, northeast slopes: on logs, 2000 m., 31486, 31545.

Ectropothecium circinatulum Ther.

Morobe District, Kaindi: on bank of stream, 2060 m., 29557.

Ectropothecium arfakense Broth. & Geh.

Purosa, Okapa area: on a log, 1950 m., 31650. Arau: on a log, 1400 m., 31927. Morobe District: Umi River, Markham Valley: on a log, 480 m., 32720.

Ectropothecium longipedunculatum Dix.

Purosa, Okapa area: on leaf-littered ground, 2000 m., 31839.

Ectropothecium buitenzorgii (Bel.) Jaeg.

Mt. Michael, northeast slopes: on a log, 31348. Kassam: on logs and rocks in a stream bed, 1370 m., 32335, 32434, in part. Arau: on a log, 1400 m., 31927a. Morobe District, Mt. Kaindi: on log, 2200 m., 29594, in part.

Ectropothecium dealbatum (H. & R.) Jaeg.

Morobe District, Botanic Gardens, Lae: on orchid roots, 200 ft., 29113.

Trachythecium verrucosum (Hpe.) Fleisch.

Purosa, Okapa area: on a branch in rain forest undergrowth, 1950 m., 31648; on rotting wood, 1950 m., 31798. Arau: on a log, 1400 m., 31908. Morobe District, Umi River, Markham Valley: on logs and rocks, 480 m., 32530, in part, 32682, in part.

Isopterygium albescens (Schwaegr.) Jaegr.

Morobe District, Botanic Gardens, Lae: on a tree-fern stem, 200 ft., 29106.

Ctenidium luzonense Broth.

Mt. Wilhelm, east slopes: on leaves of an epiphytic fern in subalpine forest, 3700 m., 29992; on a tree trunk, 2740 m., 30236.

Hylocomiaceae

Macrothamnium hylocomioides Fleisch.

Mt. Wilhelm, east slopes: on lower trunks of trees in moist forest, 2850 m., 30556.

Polytrichaceae

Pogonatum junghuhnianum (D. & M.) Bosch & Lac.
Mt. Otto, south slopes: on clayey roadbanks, 7,300 ft., Kotuni, 29123.

Pogonatum humile Bartr.
Mt. Wilhelm, east slopes: in a crevice near summit, 14,500–14,700 ft., *Collins* 29967; on ground near summit, 14,700 ft., *Collins* 29964a.

Pogonatum klossii Dix.
Mt. Otto, south slopes: on claybanks, 29122a. Morobe District, Kaindi: on clayey ground, 2060 m., 29578.

Pogonatum spurio-cirratum Broth.
Purosa, Okapa area: in small colonies in rain forest, 1950 m., 31736. Mt. Elandora, Kratke Mts.: terrestrial in forest, 2130 m., *Brass & Collins* 32166.

Polytrichum juniperinum Hedw.
Mt. Michael: alpine grasslands, 3650 m., *Brass & Collins* 31260, 31432.

Polytrichadelphus archboldii Bartr.
Mt. Wilhelm, east slopes: on open eroding banks of Pengagl Creek, 2770 m., 30408.

Dawsoniaceae

Dawsonia grandis Schleip. & Geh.
Mt. Wilhelm, east slopes: a small colony in moist, mossy forest, 2600 m., 30487. Purosa, Okapa area: in rain forest, 1950 m., 31719.

Dawsonia pullei Fleisch.
Mt. Michael: on a path in low, mossy, myrtaceous forest, 3290 m., 31419. Morobe District, Kaindi: on mossy ground in *Nothofagus* forest, 2150 m., 29633.

Dawsonia lativaginata v. d. Wijk.
Mt. Otto, south slopes: on rocks and ground in rain forest of a ravine, leaves somewhat bluish green, 2200 m., 30828.

Dawsonia beccarii Broth. & Geh.
Morobe District, Wau-Edie Creek road: on open, clayey ground, 5,800 ft., 29164; Kaindi: on open, clayey banks of a stream, 2060 m., 29625.

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STUDIES OF PACIFIC ISLAND PLANTS, XVIII
NEW AND NOTEWORTHY FLOWERING PLANTS FROM FIJI

By ALBERT C. SMITH

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STUDIES OF PACIFIC ISLAND PLANTS, XVIII[1]

NEW AND NOTEWORTHY FLOWERING PLANTS FROM FIJI

ALBERT C. SMITH

Most of the plants discussed or described in this paper were obtained during the writer's third collecting trip to Fiji in 1953–54.[2] The first set of this material is deposited in the U.S. National Herbarium; a duplicate study set is in the herbarium of the Bernice P. Bishop Museum; and eight remaining sets will shortly be distributed to world herbaria. However, earlier collections in herbaria have also been consulted and are here cited when pertinent. In this paper 18 species are described as new, and range extensions and emendations are noted for a few others. The place of deposit of specimens is indicated as follows: Arnold Arboretum (A); Bernice P. Bishop Museum (Bish); Gray Herbarium (GH); University of California, Berkeley (UC); U.S. National Herbarium (US). I am indebted to the staffs of these institutions for the privilege of studying such material, and especially to the Director of the Bishop Museum for providing permanent working space.

Musaceae

Heliconia paka A. C. Sm., sp. nov.

Heliconia bihai sensu A. C. Sm. Sargentia 1:7. 1942; sensu J. W. Parham, Pl. Fiji Isl. 259. 1964; non L.

Herba valida 2–6 m. alta; foliis saepe 3 m. longis vel longioribus glabris, petiolis crassis ad 1 m. longis, laminis lanceolatis 2–3 m. longis medium versus 30–50 cm. latis, basi rotundatis et in petiolum decurrentibus, apice obtusis, costa valida, nervis primariis inter se 0.8–1.5 cm. marginem versus abrupte curvatis; inflorescentia erecta ad 60–70 cm. longa, pedunculo et rhachide crassis 10–15 mm. diametro glabris,

[1] This paper is based on research partially supported by a grant from the National Science Foundation. Number XVII, by A. C. Smith and B. C. Stone, was published in Contr. U.S. Nat. Herb. 37:1–41, 3 pls. 1962.

[2] Smith, A. C., Botanical studies in Fiji. Ann. Rep. Smithsonian Inst. for 1954: 305–315, 12 pls. 1955. For itineraries of the two earlier trips, see Journ. New York Bot. Gard. 35:261–280. 1934; Journ. Arnold Arb. 31:138–141. 1950.

pedunculo 5–10 cm. longo, rhachide inconspicue flexuosa; bracteis primariis inter se 2–6 cm. plerumque 12–15, vagina subcoriacea saepe lenticellata marginem versus pilis brunneis 0.3–0.7 mm. longis inconspicue hispidula, lamina subcarnosa late ovato-lanceolata, 30 (inferiore)–13 (superiore) cm. longa, ad 5 cm. lata, ad apicem obtusum gradatim angustata, crasse carinata, margine scariosa, conspicue nervata, praeter margines versus proxime ut vagina pilosa ubique glabra; floribus glabris plerumque 5–8 in axillis bractearum; bracteis sub floribus e basi lata lanceolatis 6–7 cm. longis 1.5–2 cm. latis acutis multinerviis inconspicue carinatis, praeter pilos rigidos brunneos adpressos circiter 1 mm. longos ad carinam glabris; pedicellis teretibus 2–4 mm. diametro 15–25 mm. longis sub anthesi et fructu superne paullo incrassatis; tepalis liberis in vivo subcarnosis in sicco chartaceis conspicue nervatis 55–60 mm. longis, posteriore 7–9 mm. anterioribus 4–5 mm. interioribus 5–6 mm. latis; staminodio petaloideo tepalum posterius basim versus affixo, parte libera subcarnosa ovato-cucullata acuta ca. 5×5 mm.; staminibus et stylo sub anthesi quam tepalis paullo brevioribus, antheris 12–13 mm. longis obtusis, stigmate 3-lobato lobis obscure bifidis; ovario elongato-turbinato sub anthesi 10–13 mm. longo et 4–5 mm. diametro; fructu in vivo carnoso in sicco coriaceo ellipsoideo-triquetro ad 25 mm. longo et 20 mm. lato, basi obtuso, apice anguste truncato; seminibus 3 coriaceis triquetris ca. 18 mm. longis, 6–8 mm. latis, utroque subapiculatis, intus basim versus operculatis, conspicue ruguloso-tuberculatis praecipue faciebus exterioribus et carina dorsali, tuberculis obtusis vel interdum carina complanatis et 1–2 mm. eminentibus.

Type in the U.S. National Herbarium, Nos. 2191516–2191519 (4 sheets), collected in dense forest in the hills east of the Wainikoroiluva River, near Namuamua, Namosi Province, Viti Levu, Fiji, alt. 50–200 m., October 15, 1953, by A. C. Smith (No. 8900). Duplicates at Bish, etc.

ADDITIONAL SPECIMENS EXAMINED:

FIJI: VITI LEVU: Mba: Mountains near Lautoka, *Greenwood* 1303 (A, US); Mt. Evans Range, *Greenwood* 1156 (A); vicinity of Nandarivatu, *Degener* 14352 (Bish, GH, UC, US). Naitasiri: Raradawai, Wainamo-Wainisavulevu Divide, *St. John* 18263 (Bish, US); Suva Pumping Station, *Degener & Ordonez* 13988 (Bish, GH, UC, US); Central Road 8 miles from Suva, *MacDaniels* 1152 (Bish). KANDAVU: Hills above Namalata and Ngaloa Bays, *Smith* 193 (Bish). VANUA LEVU: Thakaundrove: Vatunivuamonde Mt., Savu Savu Bay region, *Degener & Ordonez* 14011 (Bish, GH, UC, US).

The local name "paka" is commonly applied to this indigenous *Heliconia,* and St. John also records it as "vava ni Viti." The plant is a fairly common component of rain forests and wet thickets at elevations from near sea level up to at least 750 m.; it is more abundant than indicated by the number of collections, as evidently collectors choose not to prepare material of what they take to be a common

coarse herb. The leaves are suitable for thatching temporary shelters and the plant is thus well known to local hunters and forest travelers. There is no indication that this species is an introduction, and no justification for referring it to the American *H. bihai* L. Degener (No. 14352) indicates that the seeds are edible when cooked, and St. John's label suggests that the flowers may be eaten raw or boiled. The collection selected as the type bears good flowers, and several of the other specimens have flowers as well as fruits. Field notes indicate that the outer bracts are red, the inner bracts dull yellow, and the fruit yellow, becoming orange when ripe.

Schumann (Pflanzenr. 1 (IV. 45):36. 1900) implies that his concept of *H. bihai* L. includes not only American plants from the West Indies and Mexico to southern Brazil, but also specimens from Samoa westward to the Moluccas or perhaps to Sumatra. The Fijian material, indeed, keys to *H. bihai* in his system. Subsequent students of *Heliconia* have realized that *H. bihai* could not logically be so inclusive. Griggs (Bull. Torrey Club 30:656. 1903) more narrowly defined *H. bihai* and suggested that it is limited to the West Indies or Guiana. According to Griggs it has an elongate peduncle and bracts mostly concealing the rachis. Thus far most of the Old World taxa lack acceptable specific epithets, but an informative discussion by Ridley (Agric. Bull. Straits Settlem. 7:129–132. 1908) provides descriptions and notes for several of them. As far as can be ascertained at present, none of the names there discussed seem to apply to the species in Fiji. Specimens are now at hand from the island groups from Samoa westward; the available material from the New Hebrides, Solomons, and New Guinea includes several undescribed species, but none of it requires comparison with *H. paka*.

The Samoan collections cited as *H. bihai* by Christophersen (Bishop Mus. Bull. 128:54. 1935) are superficially similar to my new species, but their seeds are even more coarsely and irregularly rugulose. The indument of at least some of the Samoan specimens is more abundant (on the sheaths and surfaces of the primary bracts), being present also sometimes on the pedicel and ovary. The inner perianth segments, insofar as observed, appear to have somewhat thicker and more obviously raised nerves. In view of these points, I hesitate to combine the Samoan material with *H. paka*, although subsequent study may indicate this as the correct disposition.

Cunoniaceae

Pullea perryana A. C. Sm. Journ. Arnold Arb. 33:148. 1952.

OVALAU: Summit of Mt. Ndelaiovalau and adjacent ridge, alt. 575–628 m., in dense bush and thickets of crest, *Smith* 7613 (Bish, US, etc.) (tree 12 m. high; perianth white; disk lobes rich pink; filaments and styles white).

The third collection of this species, previously known only from southeastern Viti Levu, is of interest. In inflorescence and floral characters the Ovalau material is essentially identical with the earlier collections, but its leaf blades are consistently smaller, being only 4–7×2–3.5 cm., and correspondingly less coarsely crenate. These foliage differences may be merely the result of the exposed habitat on the eastern ridge of Ovalau.

Meliaceae

Aglaia gracilis A. C. Sm. Contr. U.S. Nat. Herb. 30:489. 1952.

Viti Levu: Serua: Hills east of Navua River, near Nukusere, in dense forest, alt. 100–200 m., *Smith* 9126 (Bish, US, etc.) (simple-stemmed shrub or small tree to 5 m. high; inflorescence borne on main stem; petals dull yellow; anthers yellowish white); hills between Wainingere and Waisese Creeks, between Ngaloa and Wainiyambia, in dry forest, alt. 50–100 m., *Smith* 9551 (US) (slender tree 2 m. high; petals and filaments yellow; anthers nearly white).

This infrequently collected species has not otherwise been recorded below 750 m. The Serua collections provide the only flowering material known other than the type, with which they agree excellently in the very distinctive floral characters. However, they permit a slight amplification of the original description as follows:

Leaves up to 70 cm. long, the petiole up to 22 cm. long; leaflet blades up to 28×7 cm.; inflorescences up to 2 cm. long, the lateral branches several but inconspicuous, up to 6 mm. long.

Dysoxylum gillespieanum A. C. Sm. Contr. U.S. Nat. Herb. 30:516. 1952.

Viti Levu: Serua: Hills east of Navua River, near Nukusere, alt. 100–200 m., in dense forest, *Smith* 9105 (Bish, US, etc.) (tree 20 m. high; young inflorescence brownish green; fruit green, ellipsoid, up to 5×3.5 cm.); hills between Wainingere and Waisese Creeks, between Ngaloa and Wainiyambia, alt. 50-100 m., in dry forest, *Smith* 9381 (Bish, US, etc.) (tree 15 m. high; flower buds dull green); Namboutini, roadside near Nambukelevu, *Qoro & Kuruvoli* 13717 (Fiji Dept. Agriculture, Bish) (slender tree 8 m. high; fruit brown, oval).

The cited collections, obtained at lower elevations than the two specimens thus far known, are interesting in that they verify the position assigned to *D. gillespieanum* in my original treatment. The flowers now available indicate that the species belongs in § *Dysoxylum* and is indeed a fairly close relative of *D. lenticellare* Gillespie. No. 9381 has nearly mature inflorescences, while No. 9105 has young inflorescences and also mature fruits, somewhat larger than those originally described. Further differentiating characters based on the inflorescence may now be indicated. *Dysoxylum gillespieanum* differs from *D. lenticellare* in its compact, simply racemose (rather than branched) inflorescence, its basically 4-merous (rather than 5-merous) flowers, its disk sericeous-puberulent within (rather than glabrous),

and its solitary (rather than paired) ovules. Probably the flowers are also smaller than those described for *D. lenticellare* (Contr. U.S. Nat. Herb. 30:508. 1952), but this cannot be stressed in the absence of fully mature flowers. The new collections permit amplification of my earlier description as to foliage dimensions as well as to inflorescence:

Leaves up to 40 cm. long, the petiole to 9 cm. long, the petiolules to 25 mm. long; leaflet blades occasionally oblong-oblanceolate and up to 22×8 cm., the secondary nerves up to 16 per side; inflorescence arising from branchlets below leaves, simply racemose, in advanced bud 1.5–2 cm. long, the peduncle 2–3 mm. long; peduncle, rachis, bracts, pedicels, and calyx copiously but minutely sericeous with yellowish hairs scarcely 0.1 mm. long; flowers 10–15 per inflorescence, solitary in the axils of broadly deltoid, rounded bracts about 1×2 mm.; pedicels stout, 1–2 mm. long; calyx gamosepalous, cupuliform, slightly before anthesis about 2×3 mm., the tube minute, the limb subcarnose, irregularly 4-lobed, the lobes valvate, broadly ovate, up to 1×2 mm., rounded or obtuse at apex, the sinuses acute; petals 4, carnose, in advanced bud about 2.5 mm. long and 1.5–2 mm. broad, subacute, sericeous-puberulent without like the calyx; staminal tube short-cylindric, subcarnose, about 2 mm. long, glabrous, crenulate at apex; stamens 7 or 8, the anthers sessile, oblong, obtuse, about 0.9 mm. long; disk carnose, about 1 mm. long and 1.5 mm. in diameter, crenulate at apex, glabrous without, sparsely sericeous-puberulent within and with a few marginal setae up to 0.5 mm. long; ovary copiously yellowish sericeous with hairs about 0.2 mm. long, the locules 3, each with one ovule affixed near the middle, the style stout, terete, about 1 mm. long, glabrous, the stigma peltate, about 0.8 mm. in diameter, crenulate at margin.

Euphorbiaceae

Macaranga (§ *Adenoceras*) **caesariata** A. C. Sm., sp. nov.

Arbor gracilis ad 8 m. alta; ramulis teretibus crassis apicem versus 1–1.5 cm. diametro, pilis stramineis 1.5–2.5 mm. longis copiosissime et pervicaciter villosis; stipulis subcoriaceis elliptico-oblongis ca. 1.5 cm. longis et 1 cm. latis, apice obtusis, extus copiose villosis, intus glabris; petiolis validis 12–23 cm. longis ut ramulis villosis; foliorum laminis amplis late ovatis 25–45 cm. longis 20–35 cm. latis, basi rotundatis et late (5–9 cm.) peltatis, apice in acuminem gracilem 1–2 cm. longum angustatis, margine inconspicue crenulatis, supra glabris vel nervis et interdum venulis notabiliter setulosis, subtus nervis omnibus ut petiolo copiose setuloso-villosis ac etiam conspicue miniato-glandulosis, nervis primariis 6–8 supra leviter elevatis subtus prominentibus,

rete venularum intricato subtus prominulo; inflorescentiis ♂ copiose ramulosis ad 20 cm. longis latisque, ramulis ad nodos pilis pallidis 0.5–1 mm. longis saepe hispidulis ac etiam puberulis (pilis 0.1–0.2 mm. longis) subglabratis, bracteis majoribus lanceolato-obovatis ad 8 mm. longis et 1.5 mm. latis irregulariter patelliformi-glandulosis saepe dorso parce hispidulis; floribus sessilibus 3–8 in glomerulis, calyce sub anthesi ca. 1.2 mm. longo et 1.5 mm. diametro eglanduloso 3-lobato, lobis deltoideo-ovatis acutis, staminibus 7–11 (saepe 9), filamentis ca. 1 mm. longis, antheris transverse ellipsoideis 0.5–0.6 mm. latis; inflorescentiis ♀ minoribus sub fructu 5–7 cm. longis latisque, ramulis copiose et persistenter setuloso-puberulis (pilis 0.1–0.3 mm. longis), bracteis saepe deltoideo-lanceolatis ad 4×2 mm. stipite brevi minute brunneo-sericeis; pedicellis sub fructu 2–3 mm. longis puberulis, calyce rotato ca. 3 mm. diametro inaequaliter fisso parce sericeo; fructibus levibus copiosissime sessili-glandulosis, coccis 3.5–4 mm. diametro, stylis 2 divaricatis 1–1.5 mm. longis.

Type in the U.S. National Herbarium, Nos. 2191715 and 2191716, collected in dense forest in the hills west of Waivunu Creek, between Ngaloa and Korovou, Serua Province, Viti Levu, Fiji, alt. 50–150 m., November 23, 1953, by A. C. Smith (No. 9218). Duplicates at Bish, etc.

ADDITIONAL SPECIMENS EXAMINED:

FIJI: VITI LEVU: Serua: Hills between Waininggere and Waisese Creeks, between Ngaloa and Wainiyambia, alt. 50–100 m., in dry forest, *Smith* 9657 (Bish, US, etc.). Rewa: Mt. Korombamba, *Meebold* 16473 (Bish).

The collection selected as the type bears staminate inflorescences; I recorded the local names of "ndavo" or "mavo." No. 9657 is from a fruiting specimen, and the Meebold collection consists of a single leaf. My notes indicate the tree as slender and freely branched, 6–8 m. high, with copious thin, red latex; the staminate perianth is brick red and the anthers pale yellow.

The new species is closely related only to *M. magna* Turrill, from which it is readily distinguished by the copious and persistent indument of its branchlets, petioles, and lower surfaces of leaf blades. The corresponding indument of *M. magna* is not only sparser and fugacious, but the individual hairs are only 0.2–0.5 mm. long, whereas the hairs of the vegetative parts of *M. caesariata* are 1.5–2.5 mm. long and form a striking covering. The indument on the inflorescence branches is also more obvious in the new species, but there appear to be no very obvious floral differences. The stamens of the new species are fewer (7–11 as far as observed), as compared with 12–14 in *M. magna*.

Glochidion atalotrichum A. C. Sm., sp. nov.

Arbor monoica multiramosa 4–8 m. alta, ramulis cinereis gracilibus (apices versus 0.5–1 mm. diametro subflexuosis) juventute copiose

stramineo-hirtellis (pilis 0.5–1 mm. longis manifeste septatis 5–8-cellularibus) ac etiam copiose albo-puberulis (pilis haud 0.1 mm. longis), indumento longiore mox caduco, breviore subpersistente; stipulis deltoideo-lanceolatis glabratis 1–1.5 mm. longis mox caducis; petiolis gracilibus 2–4 mm. longis primo ut ramulis saepe pilosis mox glabratis; foliorum laminis chartaceis glabris in sicco supra fuscis subtus pallidioribus, ovato-lanceolatis, 4–7.5 cm. longis 1.5–2.5 cm. latis vel interdum minoribus, basi obtusis et in petiolum decurrentibus, apice in acuminem gracilem 1–1.5 cm. longum gradatim angustatis, margine integris vel haud undulatis, costa supra acute elevata subtus prominente, nervis secundariis utrinsecus 5–8 curvatis anastomosantibus supra subplanis subtus prominulis, rete venularum supra obscuro subtus subprominulo; inflorescentiis ♂ axillaribus breviter racemosis saepe 2-floris, rhachide 0.5–1 mm. longa, bracteis imbricatis ad 10 deltoideis subacutis glabris haud 0.5 mm. longis, pedicellis gracilibus glabris sub anthesi 3–6 mm. longis; perianthio ovoideo, segmentis 6 similibus oblongis 1.8–2 mm. longis 0.8–1 mm. latis subacutis, extus ut ramulis juvenilibus hirtellis sed interdum subglabratis; columna staminali ca. 1.2 mm. longa, antheris 3 loculis connatis ca. 0.7 mm. longis, connectivis in apices oblongos subacutos ca. 0.3 mm. longos productis; floribus ♀ forsan solitariis, pedicello, perianthii segmentis, et gynoecio ut ramulis juvenilibus hirtellis, ovario triquetro-ovoideo, columna stylari post anthesin subulata ca. 2 mm. longa, stylis 3 apicem versus liberis; capsulis depresso-globosis maturitate ad 12 mm. diametro, stylis longe persistentibus et manifeste hirtellis, valvis 3 sulcatis demum bilobatis, seminibus rubris ovoideis 3.5–5 mm. longis 2.5–4 mm. latis.

Type in the U.S. National Herbarium, No. 2191397, collected in dense forest on the northern slopes of the Korombasambasanga Range, in drainage of Wainavindrau Creek, Namosi Province, Viti Levu, Fiji, alt. 450–600 m., September 28, 1953, by A. C. Smith (No. 8747). Duplicates at Bish, etc.

ADDITIONAL SPECIMENS EXAMINED:

FIJI: VITI LEVU: Namosi: Hills north of Wainavindrau Creek, between Korombasambasanga Range and Mt. Naitarandamu, alt. 250–450 m., in dense forest, *Smith* 8463 (Bish, US, etc.). Namosi-Naitasiri boundary: Mt. Naitarandamu, alt. 800 m., *Gillespie* 3103 (A, Bish, US).

Field notes indicate the plant as a freely branched, spreading tree 4–8 m. high, with yellowish-green perianth segments. My two collections are clearly monoecious, bearing staminate flowers as well as pistillate, although the latter are scarce; No. 8463 also bears a few fruits. The Gillespie specimen bears detached fruits that appear to be fully mature.

Among the species of our area, *G. atalotrichum* is recognized by the characteristic multiseptate hairs of the young vegetative parts, which

are also often present on the perianth segments and on the gynoecium, persisting on the styles in fruit. From *G. seemannii* Muell. Arg., which it resembles superficially, the new species differs not only in its indument, but also in its long-acuminate leaf blades and its three styles.

Anacardiaceae

Pleiogynium hapalum A. C. Sm., sp. nov.

Arbor dioica gracilis 5–20 m. alta, ramulis subteretibus apicem versus 5–10 mm. diametro, partibus novellis pilis fusco-stramineis mollis patentibus simplicibus 0.2–0.5 mm. longis copiose indutis; foliis imparipinnatis (20–) 30–50 cm. longis, petiolis (3–) 4–12 cm. longis et rhachide subteretibus et copiose contumaciter pilosis; foliolis (9–) 11 vel 13, petiolulis gracilibus leviter canaliculatis 5–10 mm. longis (terminali ad 30 mm. longo) ut rhachide pilosis; foliolorum laminis chartaceis in sicco supra fuscis subtus viridescentibus inaequaliter ovatis, (6–) 8–13 cm. longis, (2.5–) 4.5–6 cm. latis (inferioribus saepe minoribus), basi inaequaliter subacutis vel obtusis et in petiolulum decurrentibus, apice acutis vel in acuminem ad 1 cm. longum cuspidatis, margine integris vel obscure undulatis, supra praeter costam et nervorum secundariorum bases pilosas glabris, subtus conspicue et persistenter pilosis (pilis ad 0.5 mm. longis praesertim costa et nervis permansis), costa supra elevata subtus prominente, nervis secundariis utrinsecus 6–10 patentibus supra planis vel prominulis subtus elevatis, rete venularum intricato supra immerso subtus haud prominulo; inflorescentiis ♂ axillaribus late paniculatis multifloris 10–30 cm. longis 4–12 cm. latis, pedunculo 2–10 cm. longo, ramulis numerosis gracilibus inferioribus 2–7 cm. longis, axibus omnibus ut foliolorum rhachide copiose pilosis, bracteis ad nodos deltoideo-oblongis obtusis 0.5–1 mm. longis subacutis extus pilosis; floribus ♂ subsessilibus laxe aggregatis vel apice ramulorum ultimorum brevium solitariis, pedicello super articulationem ad 1 mm. longo bracteas obscuras 1–3 oblongas 0.2–0.5 mm. longas inconspicue glanduloso-ciliolatas gerente; floribus glabris, calyce subrotato 1.7–3 mm. diametro, lobis submembranaceis semiorbiculari-oblongis 0.5–0.8 mm. longis 0.7–1.2 mm. latis margine glanduloso-ciliolatis, petalis plerumque 5 (raro 4 vel 6) anguste imbricatis submembranaceis oblongis 1.8–2.2 mm. longis 1.3–1.5 mm. latis apice obtusis 3–5-nervatis; disco annulari-pulvinato 1.5–2 mm. diametro manifeste crenulato; staminibus plerumque 10 (interdum 9–12), filamentis filiformi-subulatis 0.6–1.5 mm. longis, antheris ovatis versatilibus 0.5–0.7 mm. longis apice obtusis, thecis basi divergentibus; gynaecio in floribus ♂ abortivo in disco immerso, stylis rudimentariis cono inconspicuo 5–7-sulcato adnatis vel raro minute liberis; inflorescentiis ♀ quam ♂ simplicioribus similiter pilosis 3–6 cm. longis

paucifloris; perianthio ut ♂ sed calyce post anthesin incrassato, petalis ad 3×2.5 mm.; staminodiis saepe 14, filamentis 0.7–1 mm. longis reflexis, antheris minutis sterilibus; disco conspicue pulvinato carnoso incrassato; ovario oblato-sphaeroideo apice rotundato basim versus angustato, stylis crassis 7 vel 8 ca. 0.5 mm. longis e ovarii margine distali patentibus, loculis 7 vel 8, ovulis solitariis pendulis; inflorescentia sub fructu ramulis pedunculisque persistenter pilosis; drupa late turbinata 12–14 mm. alta paullo supra medium 18–20 mm. lata et ibi manifeste 7- vel 8-angulata, basi et apice rotundata.

Type in the U.S. National Herbarium, No. 2191567, collected in dense forest in the hills east of the Wainikoroiluva River, near Namuamua, Namosi Province, Viti Levu, Fiji, alt. 50–200 m., October 15, 1953, by A. C. Smith (No. 8958). Duplicates at Bish, etc.

ADDITIONAL SPECIMENS EXAMINED:

FIJI: VITI LEVU: Mba: Vicinity of Nandarivatu, *Gillespie* 3189 (Bish, GH, UC, US). Namosi: Northern slopes of Korombasambasanga Range, in drainage of Wainavindrau Creek, *Smith* 8699 (Bish, US, etc.); hills bordering Wainavindrau Creek, in vicinity of Wainimakutu, *Smith* 8531 (Bish, US, etc.); vicinity of Nanggarawai, *Gillespie* 3227 (Bish, GH, UC, US); vicinity of Namuamua, *Gillespie* 2977 (Bish, GH, UC), 3058 (Bish, GH, UC). Tailevu: Hills east of Wainimbuka River, in vicinity of Ndakuivuna, *Smith* 7164 (Bish, US, etc.). VANUA LEVU: Thakaundrove: Natewa Bay region, hills west of Korotasere, *Smith* 1940 (Bish, GH, UC, US).

Field notes indicate the plant as a slender tree 5–20 m. high, occurring in forested areas at elevations of 50–750 m.; the petals are yellow or greenish yellow, the filaments white or greenish yellow, and the anthers yellow. Pistillate inflorescences are found only on *Gillespie* 3189, fruits on *Smith* 7164, and staminate inflorescences on the other collections.

As Leenhouts has pointed out (Blumea 7:159. 1952), the correct name for the widespread tree that has long been passing as *Pleiogynium solandri* (Benth.) Engl. is *P. timoriense* (DC.) Leenh. This occurs from at least Timor through Queensland and into the Pacific as far as Tonga and the Cook Islands, being frequent in Fiji. It is characteristically glabrous, but some individuals in Fiji and Tonga (and perhaps also in Australia to judge from Engler's description in DC. Monogr. Phan. 4:255. 1883) are puberulent on the young parts of the branchlets, petiole, and leaf rachis. However, these parts bear hairs scarcely exceeding 0.1 mm. in length and they are soon glabrate. The species here described has no consequential inflorescence or fruit differences from the glabrous individuals, but the copious and persistent indument of its vegetative parts and inflorescence axes seems too striking to permit its inclusion in the widespread species.

Another species of this relationship, *P. papuanum* C. T. White (Proc. Roy. Soc. Queensl. 45:27. 1934), differs from *P. hapalum* in its smaller, glabrous leaves with fewer leaflets, its smaller ♂ flowers, and the furfuraceous gray scurfy indument of its branchlets and rachis.

Gillespie inscribed some of his collections which are cited above with a binomial apparently based on *Dracontomelum pilosum* Seem. and accredited to Engler; however, no such binomial appears to have been published. At any rate *Dracontomelum pilosum* is quite a different plant, recently referred to the synonymy of *Dysoxylum quercifolium* (Seem.) A. C. Sm. (Brittonia 14:245. 1962).

Celastraceae

Cassine vitiensis (A. C. Sm.) A. C. Sm., comb. nov.

Elaeodendron vitiense A. C. Sm. Journ. Arnold Arb. 31:289. 1950.

VITI LEVU: Serua: Hills between Waininggere and Waisese Creeks, between Ngaloa and Wainiyambia, alt. 50–100 m., in dry forest, *Smith* 9385 (Bish, US, etc.). OVALAU: Hills southeast of valley of Mbureta River, alt. 100–300 m., in dense forest, *Smith* 7450 (Bish, US, etc.).

Ding Hou (Fl. Males. I. 6:284. 1963) gives cogent reasons for combining *Elaeodendron* and *Cassine*, in which conclusions it seems advisable to follow him. The second and third collections of the apparently uncommon Fijian species show differences from the type, but these do not appear very significant. No. 9385 bears flowers that are substantially smaller than those originally described, and have the ovary only 2(rather than 3- or 4-)-locular. Fruits are present in both the newer collections. My original description may be amplified as follows:

Tree up to 20 m. high, the leaf blades up to 13 cm. long and 8.5 cm. broad; pedicels in flower often only 1.5–2 mm. long and the flowers only 5–6 mm. in diameter, the petals as small as 2.5×2 mm., the filaments as short as 0.5 mm., the anthers only 0.4 mm. broad, the ovary-locules sometimes only 2; pedicels in fruit up to 7 mm. long, the disk, stamens, and stigma subpersistent; fruits ellipsoid, up to 22 mm. long and 15 mm. broad, obtuse at base, acute or cuspidate at apex, the epicarp thin but coriaceous, smooth, the mesocarp fibrous, hard in dried fruits, 1.5–2 mm. thick, the endocarp hard and bony, 1–2 mm. thick, inconspicuously rugulose without, forming 2 separable putamens, these laterally flattened, up to 15×7×5 mm.; seed solitary, ellipsoid-lanceolate, about 12×6 mm., strongly flattened, obtuse or subacute at both ends.

Elaeocarpaceae

Elaeocarpus (§ *Blepharoceras*) **milnei** Seem. Fl. Vit. 28. 1865; A. C. Sm. Contr. U.S. Nat. Herb. 30:556. 1953.

VITI LEVU: Namosi: Northern slopes of Korombasambasanga Range, in drainage of Wainavindrau Creek, alt. 450–600 m., in dense forest, *Smith* 8731 (Bish, US, etc.).

It is a satisfaction to have available a second collection of a species otherwise known only from the type specimen, the more so as the new material agrees almost precisely with the type (*Milne* 81) and has adequate color notes. In my observation flower color provides a dependable character in *Elaeocarpus*, but it is too frequently ignored. No. 8731 has the sepals dull pink, and the petals rich pink with pale yellow apical laciniae. The new material permits the following slight amplification of my 1953 description:

Tree up to 15 m. high, the branchlets up to 17 mm. in diameter near apex; leaf blades up to 38 cm. long and 17 cm. broad, the marginal teeth often 1 cm. apart; sepals up to 11.5 mm. long and 3.5 mm. broad; petals up to 14 mm. long and 8 mm. broad, the apical lobes up to 12 in number; disk about 1 mm. high, with hairs about 0.3 mm. long; anthers with dorsal awns sometimes 0.8 mm. long; hairs of the ovary up to 0.3 mm. long, the ovules 8 per locule.

Except for the above trivia, my specimen appears identical with the type in such important characters as leaf shape, inflorescence dimensions, and indument. These details are recorded at this time primarily for discussion in reference to the following new species.

Elaeocarpus (§ *Blepharoceras*) **chionanthus** A. C. Sm., sp. nov.

Arbor gracilis ad 8 m. alta, partibus novellis pilis ferrugineis 0.4–0.6 mm. longis copiosissime hispidulo-hirtellis, ramulis subteretibus crassis apicem versus 7–10 mm. diametro demum glabratis; foliis apices ramulorum versus congestis, petiolis crassis 3–4 mm. diametro leviter canaliculatis 2–6 cm. longis persistenter hirtellis (pilis 0.2–0.3 mm. longis); foliorum laminis subcoriaceis in sicco fusco-viridibus oblongo-ellipticis, magnitudine diversis sed maturitate 25–30 cm. longis et 13–17 cm. latis, basi plerumque rotundatis (obtusis vel subcordatis), apice rotundatis vel late obtusis vel obtuse cuspidatis, margine anguste recurvatis et dentibus plerumque 1–1.5 cm. distantibus obscure calloso-apiculatis inconspicue crenatis, supra glabris vel costa obscure strigillosis, subtus copiose et pervicaciter pilosis (pilis ferrugineis vel stramineis mollibus 0.3–0.6 mm. longis costa secundariisque densissimis sed etiam lamina manifestis), costa supra valde elevata subtus prominente, nervis secundariis utrinsecus 9–13 patenticurvatis et marginem versus anastomosantibus supra paullo elevatis subtus prominentibus, rete venularum intricato utrinque prominulo;

inflorescentiis racemosis e ramulis infra folia enatis 25–35-floris, pedunculo subnullo (ad 3 mm. longo), rhachide gracili 12–16 cm. longa et pedicellis pilis 0.2–0.4 mm. longis copiose ferrugineo-setuloso-hirtellis, bracteis sub floribus lanceolatis ca. 1.5 mm. longis dense pilosis caducis, pedicellis sub anthesi crassis ca. 5 mm. longis; sepalis 5 subcarnosis lanceolatis 10–11 mm. longis ca. 3 mm. latis subacutis, extus copiose puberulis (pilis 0.1–0.2 mm. longis), intus carinatis et parce sericeis; petalis 5 basim versus incrassatis superne papyraceis, oblongo-obovatis, 11–13 mm. longis, 5–7 mm. latis, utrinque glabris vel intus basim versus obscure pilosis, apice lobis 8–10 fimbriatis, laciniis subaequalibus 1.5–2 mm. longis subacutis 1–4-nervatis; disco pulvinato ca. 1 mm. alto 5-lobato, lobis sulcatis pilis 0.2–0.4 mm. longis hispidulis; staminibus 23–25 uniseriatis 6–7 mm. longis, filamentis gracilibus 2–3 mm. longis obscure puberulis, antheris 3.8–4.2 mm. longis copiose et minute tuberculato-hispidulis, arista dorsali 0 2–0.3 mm. longa, apice ventrali rotundato; ovario lanceolato-ovoideo ut disco copiose sericeo-hispidulo, stylo subulato ca. 5 mm. longo superne glabro, ovarii pariete incrassato, loculis 2, ovulis in quoque loculo 8 biseriatis.

Type in the U.S. National Herbarium, Nos. 2191946 and 2191947, collected in dense forest in hills west of Waivunu Creek, between Ngaloa and Korovou, Serua Province, Viti Levu, Fiji, alt. 50–150 m., December 7, 1953, by A. C. Smith (No. 9495). Duplicates at Bish, etc.

Field notes indicate the plant to be a slender tree to 8 m. high, with petals and filaments pale green, becoming pure white, the anthers yellow, the gynoecium pale green, and the largest observed leaf blades up to 30×17 cm. Small leaf blades are often mixed with the larger ones on the same shoot. The new species is closely related only to *E. milnei* Seem., from which it differs in several characters best summarized as follows:

Indument comparatively sparse and short (hairs of various parts usually less than 0.2 mm. long, the leaf blades essentially glabrous beneath); leaf blades obovate, gradually narrowed toward base; petals rich pink, with pale yellew laciniae; anthers with dorsal awns 0.5–0.8 mm. long . . . . . **E. milnei**

Indument comparatively copious and long (hairs of various parts 0.2–0.6 mm. long, the leaf blades densely and persistently pilose beneath); leaf blades oblong-elliptic, usually rounded at base; petals pure white at anthesis; anthers with dorsal awns 0.2–0.3 mm. long . . . . . **E. chionanthus**

Melastomataceae

Astronidium pallidiflorum A. C. Sm., sp. nov.

Arbor ad 15 m. alta, partibus novellis, ramulis petiolisque pilis capitato-glandulosis graciliter stipitatis 0.1–0.3 mm. longis copiose ferrugineo-pubescentibus; ramulis apicem versus 3–7 mm. crassis et ibi complanato-quadrangularibus; petiolis gracilibus 1.5–2 mm.

diametro subteretibus 3–5 cm. longis, laminis crasso-chartaceis oblongo-lanceolatis 13–23 cm. longis 4–7.5 cm. latis, supra olivaceis et nervis principalibus ut petiolis pubescentibus demum glabratis, subtus praecipue nervis copiose pilosis (pilis clavatis ad 0.5 mm. longis vel superficie interdum ad 0.8 mm. longis), basi obtusis, apice in acuminem 1.5–2 cm. longum calloso-subacutum gradatim angustatis, margine dentibus calloso-acutis manifestis 0.5–1.5 cm. distantibus crenulatis, 5-nerviis, nervis e basi adscendentibus, exterioribus 2 comparate inconspicuis et 1–2 mm. intra marginem, costa et nervis 2 interioribus supra subplanis subtus prominentibus, venulis transversis et rete venularum laxo supra planis subtus prominulis; inflorescentia terminali trichotome cymosa sessili e basi 3-divisa ad 13 cm. longa et 20 cm. lata, ramulis crassis conspicue complanatis et pedicellis et calyce ut partibus novellis copiose pubescentibus, bracteis bracteolisque mox caducis non visis, floribus apices ramulorum ultimorum versus 2–5 aggregatis, pedicellis crassis 1–1.5 mm. longis; calyce submaturo cupuliformi 4–4.5 mm. longo et diametro apice lobis plerumque 10 subdeltoideis obtusis ca. 0.5 mm. longis inaequabiliter fisso; petalis glabris in floribus submaturis 5 oblongis ad 4×2.5 mm. apice rotundatis, staminibus 10 valde inflexis, filamentis ligulatis ca. 3 mm. longis, antheris oblongis ca. 3 mm. longis apice conspicue recurvatis, calcari basilari conspicuo ca. 0.8 mm. longo; stylo tereti petalis subaequali, ovarii loculis 5, placentis clavatis, ovulis numerosissimis.

Type in the U.S. National Herbarium, No. 2191790, collected in dense forest in the hills west of Waivunu Creek, between Ngaloa and Korovou, Serua Province, Viti Levu, Fiji, alt. 50–150 m., November 26, 1953, by A. C. Smith (No. 9313). Duplicates at Bish, etc.

Field notes indicate the plant as a tree 15 m. high, with pale greenish white petals, filaments, anthers, and style. The new species is closely related only to *A. kasiense* A. C. Sm., with which it has in common a copious indument of clavate hairs, these being very different from the much longer, subulate hairs of *A. storckii* Seem., the only other Fijian species of this general affinity. The principal points of difference between the new species and *A. kasiense* are summarized as follows:

Indument of young parts, petioles, inflorescence branches, etc., composed of hairs usually 0.2–0.5 mm. long; leaf blades ovate-elliptic, 7–12 cm. broad, rounded to obscurely subcordate at base, the fourth and fifth nerves 4–5 mm. within the margin and conspicuously connected by transverse veinlets to an obvious submarginal nerve; flowers (as far as known) 4-merous . **A. kasiense**

Indument of young parts, petioles, inflorescence branches, etc., comparatively close, composed of hairs usually 0.1–0.3 mm. long; leaf blades oblong-lanceolate, 4–7.5 cm. broad, obtuse at base, the fourth and fifth nerves submarginal, 1–2 mm. within the margin and lacking exterior veinlets; flowers (as far as known) 5-merous . . . . . **A. pallidiflorum**

Medinilla subviridis A. C. Sm. Journ. Arnold Arb. 33:101. 1952.

Viti Levu: Namosi: Hills north of Wainavindrau Creek, between the Korombasambasanga Range and Mt. Naitarandamu, *Smith* 8487 (Bish, US, etc); northern slopes of Korombasambasanga Range, in drainage of Wainavindrau Creek, *Smith* 8748 (Bish, US, etc.). Serua: Hills between Waininggere and Waisese Creeks, between Ngaloa and Wainiyambia, *Smith* 9541 (Bish, US, etc.).

The three cited collections of this supposedly rare plant, formerly known from a single locality near Mt. Tomanivi, extend the known range southward in Viti Levu, and downward to the low elevation of 50–100 m. recorded for No. 9541. Color notes are remarkably consistent with those recorded in the original description. However, it may be noted that the petioles of the larger leaves are sometimes inconspicuous and only 2 mm. long, the blades themselves may be as large as 17×8 cm., and the inflorescence may be up to 10 cm. long.

Medinilla spectabilis A. C. Sm., sp. nov.

Frutex alte scandens ubique mox glaber sed partibus novellis parce furfuraceo-puberulis (pilis stramineo-ferrugineis 0.1–0.3 mm. longis multicellularibus lateraliter brevi-calcaratis vel obscure plumulosis), ramulis gracilibus subteretibus, internodiis plerumque 2–4 cm. longis; foliis similibus vel disparibus; foliis majoribus: petiolis gracilibus leviter canaliculatis 13–25 mm. longis, laminis maturis chartaceis vel papyraceis in sicco fusco-olivaceis ellipticis, 6–12 cm. longis, 3.5–6.5 cm. latis, basi obtusis et in petiolum breviter decurrentibus, apice obtusis vel in acuminem ad 5 mm. longum obtuse cuspidatis, plerumque e basi 7-nerviis, nervis superioribus et costa e basi liberis vel ad 5 mm. conjunctis supra subplanis subtus elevatis, nervis aliis debilioribus, marginalibus interdum inconspicuis, venulis supra immersis subtus prominulis vel planis; foliis minoribus: petiolis saepe haud 3 mm. longis, laminis interdum 2.5×2 cm., in forma et textura majoribus similibus; inflorescentiis axillaribus vel e ramulis infra folia orientibus pauciramosis, racemosis vel divaricato-cymosis, 5–25 cm. longis latisque, ramulis gracilibus in vivo molliter carnosis in sicco saepe complanatis, internodiis 10–17 mm. longis; bracteis e nodis 2 vel 3 membranaceis vel papyraceis elliptico-oblongis, 12–20 mm. longis, 5–12 mm. latis, basi et apice rotundatis, sessilibus; floribus e nodis 1–3, pedicellis gracilibus sub anthesi 5–10 mm. longis; bracteolis apice pedicellorum 2 florem plus minusve obtegentibus late vel manifeste imbricatis, textura et colore bracteis similibus, elliptico-suborbicularibus, 18–22 mm. longis, 13–15 mm. latis, basi obtusis, apice rotundatis, 7–9-nervatis, rete venularum teneri; calyce in vivo subcarnoso, hypanthio cupuliformi 5–7 mm. longo et diametro, basi obtuso et minute stipitato, ut pedicello obscure disperse-glanduloso (glandulis haud 0.05 mm. longis minute stipitatis), limbo erecto membranaceo 2–3 mm. longo integro, dentibus 4 obsoletis submar-

ginalibus; petalis 4 membranaceis late obovatis, 17–20 mm. longis, 14–17 mm. latis, apice rotundatis vel obscure retusis, basi late obtusis, multinerviis; staminibus 8, filamentis gracilibus ligulatis 6–7 mm. longis basi haud 0.5 mm. latis, antheris oblongis 4.5–5 mm. longis basi manifeste trilobulatis (lobis anterioribus ca. 0.5 mm. longis, posteriore minore), apice in tubulum 0.5–1 mm. longum poro introrso-terminali dehiscentem angustatis; stylo tereti subcarnoso 10–12 mm. longo, stigmate minuto.

Type in the U.S. National Herbarium, Nos. 2191067 and 2191068, collected in dense forest in the hills east of Somosomo, west of the old crater occupied by a small swamp and lake, Taveuni, Fiji, alt. 660–900 m., August 18, 1953, by A. C. Smith (No. 8362). Duplicates at Bish, etc.

The specimens were collected from a high-climbing liana and were noted as follows: Inflorescence arising from stem near base, or sometimes associated with leaves; inflorescence branches, bracts, and bracteoles magenta; calyx white, suffused with pink; petals pale pink; filaments and style white; anthers rich blue, the basal lobes yellow.

The *tangimauthia* of Fijian legend (*M. waterhousei* Seem.) is often considered the most beautiful indigenous plant of the archipelago; it appears limited to the summit ridge of Taveuni and to Mount Seatura on Vanua Levu. (A color photograph was recently published as the frontispiece of J. W. Parham's Plants of the Fiji Islands, 1964.) To find another spectacular *Medinilla* near the "lake" of Taveuni was a delightful surprise, the more so as the second species is nearly, if not quite, as exquisite as the *tangimauthia*. However, it is instantly distinguished, although not reasonably allied to any other species. Our new plant most strikingly differs from *M. waterhousei* in the color of its inflorescence parts and petals, and particularly in having its flowers clasped by two imbricate bracteoles, rather than by the strictly opposed and often obcordate bracteoles so characteristic of *M. waterhousei*. Differences between the two species may be summarized as follows:

Leaves of mature plants isomorphic; leaf blades 4–8×2.5–4 cm., attenuate to acute at base, 3- or 5-nerved; inflorescence branches, bracts, bracteoles, and pedicels brilliant red or scarlet; pedicels 15–25 mm. long at anthesis; flower-subtending bracteoles strictly opposed, ovate, 23–35×15–30 mm., rounded or subcordate at base; flowers comparatively large, the petals white, 23–26×20–25 mm.; filaments broadly ligulate, 1.2–1.5 mm. broad, 8–10 mm. long; anthers 7–8 mm. long, with only the posterior basal lobe obvious; style 20–22 mm. long . . . . . **M. waterhousei**

Leaves of mature plants isomorphic or dimorphic; leaf blades of larger leaves 6–12×3.5–6.5 cm., obtuse at base, usually 7-nerved; inflorescence branches, bracts, bracteoles, and pedicels magenta or pink; pedicels 5–10 mm. long at anthesis; flower-subtending bracteoles obviously imbricate, elliptic-orbicular, 18–22×13–15 mm., obtuse at base; flowers smaller, the petals pale pink,

17–20×14–17 mm.; filaments about 0.5 mm. broad, 6–7 mm. long; anthers 4.5–5 mm. long, obviously 3-lobulate at base; style 10–12 mm. long. **M. spectabilis**

Medinilla decora A. C. Sm., sp. nov.

Frutex scandens, partibus novellis, ramulis, petiolis inflorescentiae ramulisque ferrugineo-furfuraceis (pilis 0.1–0.4 mm. longis multicellularibus lateraliter brevi-calcaratis interdum ad nodos 0.8 mm. longis), ramulis subteretibus gracilibus, internodiis 3–4 cm. longis; foliis subsimilibus, petiolis gracilibus leviter canaliculatis 2–4 cm. longis, laminis chartaceis in sicco fusco-olivaceis subtus viridescentibus, elliptico-lanceolatis, (6–) 8–14 cm. longis, (2.5–) 4–6 cm. latis, basi longe attenuatis et in petiolum gradatim decurrentibus, apice obtusis vel obtuse cuspidatis, margine anguste recurvatis subintegris vel obscure crenulatis, 5-nerviis, nervis superioribus cum costa 1–3 cm. conjunctis supra leviter elevatis subtus prominentibus, nervis inferioribus intra marginem 2–3 mm. paullo debilioribus, venulis transversis subtus prominulis, rete venularum immerso; inflorescentia axillari solitaria laxa pauciflora 3–8 cm. longa, pedunculo 3–20 mm. longo et rhachide gracilibus; bracteis 2–4 e nodis papyraceis oblongo-lanceolatis, 3–5 mm. longis, 0.6–1.5 mm. latis, apice obtusis, furfuraceis vel puberulis; floribus 2–4 e nodis, pedicellis gracilibus 3–6 mm. longis; bracteolis apice pedicellorum binis membranaceis calycem obtegentibus ellipticis, 6–7 mm. longis, ca. 4 mm. latis, 5–7-nervatis, apice rotundatis, utrinque parce puberulis subglabratis; calyce 4–5 mm. longo et apice diametro, hypanthio cupuliformi, limbo suberecto submembranaceo 1–1.5 mm. longo margine integro, dentibus 4 minutis submarginalibus; petalis 4 membranaceis glabris obovatis sub anthesi 7–8 mm. longis et 6–7 mm. latis, apice rotundatis vel subretusis et obscure mucronulatis, 5-nerviis; staminibus 8 glabris, filamentis gracilibus ligulatis 3–3.5 mm. longis, antheris oblongis 1.7–2 mm. longis, basi trilobulatis (lobis 2 anterioribus ca. 0.5 mm. diametro, posteriore paullo minore), apice obtusis poro unico terminali dehiscentibus; stylo filiformi 6–7 mm. longo, stigmate minuto.

Type in the U.S. National Herbarium, No. 2191868, collected in dry forest in the hills between Wainingere and Waisese Creeks, between Ngaloa and Wainiyambia, Serua Province, Viti Levu, Fiji, alt. 50–100 m., November 30, 1953, by A. C. Smith (No. 9398). Duplicates at Bish, etc.

The specimens were collected from a high-climbing liana; the bracts and pedicels are green, the bracteoles dull pink, the calyx pale pink, the petals rich pink, the filaments and style pink-tinged, and the anthers purple, yellow at base. Color of inflorescence parts in *Medinilla*, although perhaps not basically very significant, often provides dependable differentiating characters and clues to morphological differences.

The new species is closely related only to *M. kandavuensis* A. C. Sm.,

which it resembles in foliage and pubescence, although the indument of the Serua plant is somewhat more obvious and persistent. *Medinilla decora* differs in its smaller flower-subtending bracteoles and especially in its smaller flowers; the calyx of *M. kandavuensis* is 8–9 mm. long; the petals are 12–13×10–11 mm.; the anthers are 4–5 mm. long with the posterior basal lobe slightly larger than the anterior ones; and the style is 12–13 mm. long.

From *M. rhodochlaena* A. Gray, which more nearly suggests the new species in its floral dimensions, *M. decora* differs in its consistently isomorphic leaves, the blades of which are thinner in texture and longer attenuate at base. In inflorescence characters, *M. rhodochlaena* as compared with the new species has broader bracts, flower-subtending bracteoles that are comparatively thick in texture and orbicular or reniform rather than elliptic, and a slightly smaller calyx at anthesis. Gray's species, now known from abundant material, has richly colored inflorescences, the inflorescence bracts and bracteoles being rich pink to purple red (rather than green and dull pink respectively in the new species); its calyx is also a deeper pink.

Medinilla ovalifolia (A. Gray) A. C. Sm., comb. nov.

Anplectrum ovalifolium A. Gray, Bot. U.S. Expl. Exped. 1:597. 1854.
Medinilla amoena Seem. Fl. Vit. 88. 1865.
Medinilla parvifolia Seem. Fl. Vit. 89. 1865.
Allomorpha ovalifolia Triana, Trans. Linn. Soc. 28:74. 1871.

The type specimen of *Anplectrum ovalifolium* (US 47676) was collected by the U.S. Exploring Expedition in the vicinity of Mbua Bay, Province of Mbua, Vanua Levu, Fiji. The available material was taken from a plant in bud, and apparently from a branch exposed to sun. In foliage this specimen is very similar to *Smith* 1671, also from Mbua (summit of Mt. Seatura). The form represented by these two specimens is a fairly atypical form of the species usually referred to *M. amoena* Seem., in that its leaf blades are nearly rounded at base. But in all other respects the form must be placed with *M. amoena*, and it fits my description of that species in Sargentia 1:85. 1942. As the specific epithet is available in *Medinilla*, I see no way to avoid a new combination based on *Anplectrum ovalifolium* to replace the frequently collected and well known *M. amoena*. More complete synonymy, a description, and citations of specimens are found in my 1942 publication.

Araliaceae

Polyscias culminicola A. C. Sm., sp. nov.

Arbor ad 8 m. alta, ramulis crassis et petiolorum basibus parce stramineo-puberulis mox glabratis; foliis ad apices ramulorum congestis imparipinnatis multijugis 30–40 cm. longis, petiolo 5–9 cm.

longo supra complanato basi incrassato sed haud alato, rhachide subtereti; foliolis 19–23, petiolulis gracilibus canaliculatis 4–6 (terminali ad 15) mm. longis, laminis in sicco chartaceis fusco-olivaceis, ovato-ellipticis lateralibus manifeste falcatis, 5–7 cm. longis (inferioribus minoribus), 2.5–3 cm. latis, basi inaequilateraliter obtusis vel rotundatis, apice subacutis, margine integris paullo incrassatis, costa supra paullo elevata subtus prominente, nervis secundariis utrinsecus plerumque 6–11 patentibus margines versus curvatis et anastomosantibus utrinque planis vel subtus prominulis, rete venularum immerso; inflorescentiis terminalibus racemoso-paniculatis, ad 23 cm. longis et 18 cm. latis, inflorescentiae pedunculo brevi, rhachide, ramulis, umbellarum pedunculis pedicellisque stramineo-puberulis (pilis patentibus pluricellularibus glandulosis 0.1–0.2 mm. longis); umbellarum pedunculis gracilibus 1–2.5 cm. longis interdum infra medium minute bibracteatis, bracteis sub floribus oblongis obtusis 0.5–0.7 mm. longis puberulis caducis; floribus in umbellulis 11–32 dense aggregatis, pedicellis sub anthesi gracilibus 3–4 mm. longis infra flores paullo incrassatis et articulatis; calyce obconico sub anthesi 1.5–2 mm. longo et apice 2–2.5 mm. diametro, limbo minuto obscure 5-denticulato, disco subcupuliformi carnoso; petalis 5 oblongo-deltoideis sub anthesi 2.5–3 mm. longis ca. 1.5 mm. latis, apice acutis et cucullatis, intus obscure carinatis; staminibus 5, filamentis subcarnosis teretibus 1–1.5 mm. longis, antheris oblongis 2–2.3 mm. longis apice rotundatis, thecis basi liberis; stylis 2 fere ad basim liberis carnosis subacutis ca. 1.5 mm. longis.

Type in the U.S. National Herbarium, No. 1965344, collected in crest forest on a wind-swept ridge, northern slopes of Mt. Namendre, east of Mt. Koromba (Pickering Peak), Mba Province, Viti Levu, Fiji, alt. 750–900 m., May 27, 1947, by A. C. Smith (No. 4514). Duplicates at A, Bish, etc.

Although the new species bears a superficial resemblance to *P. joskei* Gibbs, it clearly differs in its umbellate flowers, those of *P. joskei* being individually scattered on the ultimate inflorescence branches. *Poyscias joskei* further differs from *P. culminicola* in lacking the minute glandular indument described above, in having its leaflets only 7–15 and with blades that are not strongly falcate, only slightly inequilateral at base, and obviously undulate-serrulate, and in its 4-merous flowers that are borne on pedicels less than 2 mm. long. A local name recorded for the new species is "sawira."

Schefflera (§ *Heptapleurum*) **euthytricha** A. C. Sm., sp. nov.

Arbor gracilis 5–6 m. alta, ramulis teretibus crassis apices versus 1–1.5 cm. diametro, partibus novellis crasse et conspicue hirsutis (pilis saepe 5–10 mm. longis, partibus vegetativis demum caducis sed nodis, petiolis, et foliolorum costa illic persistentibus, inflorescentia

pervicacibus); foliis digitatis mox glabratis, petiolis crassis subteretibus 21–30 cm. longis, basi in vaginam coriaceam 2–3 cm. latam incrassatis, ligula obtusa ad 1 cm. longa; foliolis 7–9, petiolulis in sicco rugulosis 2–6.5 cm. longis, laminis subcoriaceis in sicco fusco-olivaceis subtus pallidioribus, elliptico- vel oblongo-oblanceolatis, 18–27 cm. longis, 7–10 cm. latis, basi inaequilateraliter obtusis vel subacutis, apice in acuminem calloso-obtusum 5–10 mm. longum cuspidatis, margine irregulariter et inconspicue crenato-serrulatis (dentibus saepe 2 vel 3 per cm. antrorse calloso-apiculatis), costa valida supra elevata subtus prominente, nervis secundariis utrinsecus 12–15 erecto-patentibus marginem versus copiose anastomosantibus supra subplanis subtus valde elevatis, rete venularum subimmerso vel interdum subtus prominulo; inflorescentia apices ramulorum versus laterali paniculato-racemosa ad 80 cm. longa et lata, pedunculo, rhachide, et ramulis copiose et conspicue hirsutis (pilis brunneis e basi crassa 0.1–0.15 mm. diametro tereti-filiformibus multicellularibus superne obtortis, pedunculo ad 9 mm. rhachide 3–6 mm. ramulisque 2–3 mm. longis), pedunculo 4–16 cm. longo bracteas 1 vel 2 subcoriaceas ad 4 cm. longas saepe gerente, rhachide tereti 2–3 mm. diametro, ramulis secundariis 12–25 gracilibus sub anthesi 17–40 cm. longis; bracteis sub ramulis papyraceis lanceolatis 25–35 mm. longis basi 4–6 mm. latis apice subulatis multinerviis, extus copiose hirsutulis, intus glabris vel parce tomentellis; umbellulis numerosis 2–15 mm. distantibus, bracteis sub umbellis 5–10×2–2.5 mm. eis majoribus subsimilibus; umbellularum pedunculis gracilibus 3–10 mm. longis parce hirtellis vel glabratis infra medium 1- vel 2-bracteolatis et apice pluribracteolatis (bracteolis lanceolatis 0.5–3 mm. longis acutis parce hispidulo-tomentellis); floribus 5–10 per umbellulam glabris vel interdum calycis lobis et petalis inconspicue setulosis, pedicellis sub anthesi 1–4 mm. longis; calyce cupuliformi ca. 1 mm. longo et 2 mm. diametro 5–dentato, dentibus deltoideis acutis 0.3–0.4 mm. longis; petalis 5 deltoideo-ovatis 1.4–1.6 mm. longis 1–1.2 mm. latis, apice acutis et cucullatis, intus obscure carinatis; staminibus 5, filamentis gracilibus 0.5–0.7 mm. longis, antheris ellipsoideis 0.6–0.8 mm. longis apice rotundatis, thecis basi liberis; ovario apice subplano, stylis 5 liberis minutis sub anthesi 0.1–0.2 mm. longis, ovulis solitariis pendulis.

Type in the U.S. National Herbarium, Nos. 2191526 and 2191527, collected in dense forest in the hills east of the Wainikoroiluva River, near Namuamua, Namosi Province, Viti Levu, Fiji, alt. 50–200 m., October 15, 1953, by A. C. Smith (No. 8908). Duplicates at Bish, etc.

ADDITIONAL SPECIMENS EXAMINED:

FIJI: VITI LEVU: Serua: Hills between Navua River and Wainiyavu Creek, near Namuamua, in dense forest, alt. 100–200 m., *Smith* 8983 (Bish, US).

Field notes indicate that the plant is a slender tree to 5 or 6 m. high; the inflorescence is lateral near the apices of branchlets; the tomentum of the inflorescence is dull brown; the calyx, petals, and filaments are greenish white, and the anthers white. A local name referred to No. 8908 was "sole tangane."

Among Fijian species, *Schefflera euthytricha* is closely allied only to the abundant *S. vitiensis* (A. Gray) Seem., but that species lacks the extraordinary, large, spreading, many-celled hairs that cover the younger vegetative parts of the new species and persist so conspicuously on its inflorescence. The rachis and branches of the inflorescence of *S. vitiensis*, if not entirely glabrous, are merely furfuraceous-tomentellous with inconspicuous, irregular hairs scarely 0.1 mm. long. Furthermore, the primary bracts of its inflorescence are subcoriaceous and comparatively small (3–15 mm. long), while its umbel-subtending bracts are usually only 1–3 (rarely 6) mm. long.

In respect to its remarkable indument, the new species is more suggestive of *S. samoensis* (A. Gray) Harms, which has similar vegetative hairs, these sometimes also occurring on the inflorescence; however, such hairs are comparatively sparse and do not exceed 2–3 mm. in length. In size of inflorescence bracts, *S. samoensis* resembles *S. vitiensis* rather than *S. euthytricha*. In having its leaflet blades conspicuously and closely apiculate-serrate, and in having 6 or 7 styles, *S. samoensis* differs from both the Fijian species of this alliance.

Myrsinaceae

Tapeinosperma ampliflorum A. C. Sm., sp. nov.

Arbor gracilis 4–10 m. alta inflorescentiis exceptis glabra (sed partibus novellis parce et obscure glanduloso-puberulis), ramulis cinereis subteretibus apices versus 4–8 mm. diametro; petiolis crassis semiteretibus 7–12 mm. longis fere ad basim angulatis, laminis subcoriaceis in sicco fuscis immerso-glandulosis obovato-ellipticis, (10–) 12–20 cm. longis, (3.5–) 5–8 cm. latis, basi attenuatis et in petiolum longe decurrentibus, apice obtusis vel rotundatis, margine integris et anguste recurvatis, costa valida supra subplana subtus prominente, nervis lateralibus primariis utrinsecus (12–) 15–20 patentibus margines versus anastomosantibus utrinque inconspicue prominulis, rete venularum subimmerso; inflorescentiis apices ramulorum versus lateralibus compacte paniculatis sub anthesi ad 6 cm. longis et 4 cm. latis (sub fructu ad 9×6 cm.), pedunculo (1–3 cm. longo), rhachide ramulisque lateralibus crassis angulatis ut pedicellis pilosis sed demum glabratis; floribus 3–6 apices ramulorum brevium (2–10 mm.) lateralium versus laxe aggregatis, bracteis oblongis obtusis 2–3 mm. longis margine ut calycis lobis ciliolatis mox caducis, pedicellis crassis

(ad 1.5 mm. diametro) subteretibus sub anthesi 1–2 mm. longis puberulis (pilis fusco-brunneis glandulosis patentibus 0.05–0.1 mm. longis); calyce cupuliformi sub anthesi 3.5–4 mm. longo 4.5–5 mm. diametro alte 5-lobato ut pedicellis glanduloso-piloso, lobis late imbricatis ovatis 2–3 mm. longis 2.5–4 mm. latis apice cuspidatis margine conspicue ciliolatis (pilis multicellularibus 0.2–0.3 mm. longis saepe obscure glandulosis); corolla carnosa immerso-nigro-glandulosa subrotata fere ad basim 5-lobata, lobis late imbricatis ovatis 3–4 mm. longis latisque obtusis; staminibus corollae faucibus insertis, filamentis brevibus, antheris deltoideo-ovoideis 1.5–1.8 mm. longis obtusis, connectivo crasso immerso-glanduloso; ovario sub anthesi conico ca. 1 mm. longo conspicue immerso-glanduloso in stylum aequilongum attenuato, stigmate truncato, placenta ovoidea apice acuta, ovulis 4; pedicellis sub fructu ad 5 mm. elongatis, calyce demum rotato 5–7 mm. diametro persistente, fructibus subgloboso-obovoideis 7–9 mm. diametro apice conico-subacutis basi obtusis, pericarpio in sicco coriaceo 1–1.5 mm. crasso, semine 1.

Type in the U.S. National Herbarium, No. 2192113, collected in dense forest in the hills east of the Navua River, near Nukusere, Serua Province, Viti Levu, Fiji, alt. 100–200 m., October 29, 1953, by A. C. Smith (No. 9102). Duplicates at Bish, etc.

ADDITIONAL SPECIMENS EXAMINED:

FIJI: VITI LEVU: Namosi: Northern slopes of Korombasambasanga Range, in drainage of Wainavindrau Creek, in dense forest, alt. 450–600 m., *Smith* 8743 (Bish, US, etc.). Serua: Vatutavathe, vicinity of Ngaloa, in forest, alt. 0–150 m., *Degener* 15176 (A, Bish, UC, US, etc.).

The cited specimens are from often slender trees 4–10 m. high; the bracts and flower buds are dull pink and the fruits dull brown.

Gillespie (Bishop Mus. Bull. 74:8. 1930) has noted that the differentiation between *Tapeinosperma* and *Discocalyx* based on the number and arrangement of ovules is not satisfactory in the Fijian species referred to these genera. Maintenance of the two genera should be based on other characters, but a decision whether to retain *Discocalyx* (the later name) requires monographic reconsideration.

Although it has a reduced number of ovules, *T. ampliflorum* is allied to species that have been placed in *Tapeinosperma*. From *T. clavatum* Mez it differs in its compact inflorescence, much larger flowers, deeply lobed calyx, and closer but basically similar inflorescence indument. In flower size, *T. chloranthum* A. C. Sm. more closely approximates the new species, but its inflorescence rachis, branches, pedicels, and calyx have a comparatively thick and tangled tomentum (of many-celled hairs 0.2–0.4 mm. long). Another species of this general relationship, *T. greenwoodii* A. C. Sm., differs from the new species in its ample inflorescence with much smaller flowers. The four species here mentioned have the ovules either 2, 3, or 4.

Rubiaceae

Squamellaria major A. C. Sm., sp. nov.

Frutex epiphyticus partibus novellis et corolla exceptis glaber, basi incrassato-tuberosus, tubere ellipsoideo ad 40 cm. longo intus cuniculis a formicis inhabitato, partibus novellis et stipularum cicatricibus pilis brunneo-stramineis debilibus ad 1 mm. longis pluricellularibus parce hirtellis, ramulis rugulosis crassis superne 4–8 mm. diametro, stipulis intrapetiolaribus mox caducis; foliis pro genere magnis subsessilibus, petiolis crassis complanatis (ad 4 mm. lato) subnullis vel ad 5 mm. longis, laminis crasso-chartaceis in sicco fusco-olivaceis oblongo-oblanceolatis, (8–) 12–17 cm. longis, (3–) 4–6.5 cm. latis, basi obtusis et subito in petiolum decurrentibus, apice rotundatis vel eroso-cuspidatis, margine scariosis integris vel undulatis, costa valida utrinque prominente, nervis secundariis utrinsecus 5–7 valde adscendentibus margines versus anastomosantibus utrinque conspicue elevatis, rete venularum laxo irregulari utrinque subprominulo; inflorescentiis axillaribus cylindrico-tuberculiformibus, rhachide ad 10 mm. longa et 4 mm. diametro videtur apice 6–10-flora, bracteis sub floribus scariosis late deltoideis obtusis ad 1×2 mm. mox caducis; floribus subsessilibus, pedicello subnullo vel sub anthesi 1–2 mm. longo; calyce subcarnoso cupuliformi sub anthesi 3–4 mm. longo, basi in pedicellum obscurum angustato, limbo erecto apice 4–5 mm. diametro integro vel obscure 4-denticulato; corolla tenuiter carnosa elongato-tubuloso-clavata maturitate 35–45 mm. longa, basim versus 3.5–4 mm. diametro, superne incrassata, extus tubo obscure puberula sed superne et lobis pilis albidis debilibus 0.1–0.3 mm. longis manifestius hirtella, intus glabra; corollae tubo 2–4 mm. supra basim squamulis 4 aucto, eis membranaceis antrorse semiorbicularibus ca. 0.5 mm. longis et 1–1.5 mm. latis, margine pilis patentibus albidis 0.5–1 mm. longis copiose barbatis; corollae lobis 4 oblongis sub anthesi 7–8 mm. longis 2–2.5 mm. latis subacutis demum reflexis; staminibus 4 corollae faucibus affixis, filamentis subteretibus 3–5 mm. longis, antheris oblongis versatilibus 5.5–6 mm. longis et ca. 1.5 mm. latis utrinque obtusis filamento medium versus affixis, thecis inferne liberis; disco annulari-pulvinato carnoso ad 0.5 mm. alto et 2 mm. diametro; stylo filiformi sub anthesi quam corolla paullo longiore, stigmate subpeltato vel discoideo-cupulari 1.2–1.4 mm. diametro apice depresso margine membranaceo reflexo, ovario 4-loculari, ovulis solitariis e basi erectis; fructibus juvenilibus ellipsoideis calycis limbo persistente suberecto coronatis.

Type in the U.S. National Herbarium, No. 2191043, collected in dense forest on the slopes of Mt. Manuka, east of Wairiki, Taveuni, Fiji, alt. 300–600 m., August 14, 1953, by A. C. Smith (No. 8323). Duplicates at Bish, etc.

Field notes indicate the plant as an epiphytic shrub, with an ellipsoid tuber up to 40 cm. long and with ant-inhabited canals; the calyx tube is white, pink-tinged, with the limb green at margin; the corolla is white, faintly pink-tinged distally within; the filaments are white and the anthers pinkish; and the style is pale pink.

As noted by Beccari in his remarkable study of myrmecophilous plants (Malesia 2:1–284. *pls. 1–65.* 1884–86), the two Fijian species that comprise his genus *Squamellaria* (op. cit., 228. 1886) are amply distinct from *Hydnophytum* and *Myrmecodia* in the barbate scales within the corolla tube and in the entire and very different stigma. Although Beccari implied that the species of *Squamellaria* are not associated with ants, this was due only to the inadequately noted specimens available to him. In my observation, all three species of the genus now known have tubers with ant-inhabited canals, similar to those of *Hydnophytum;* this is borne out by J. W. Parham (Plants of the Fiji Islands, 209. 1964).

The new species is at once distinguished from its two congeners by its much larger leaf blades, with conspicuous ascending secondary nerves, and by its large flowers. The largest leaf blades noted for the earlier species do not exceed 12 by 3 cm., nor the largest corollas 3 cm. in length. Both *S. imberbis* (A. Gray) Becc. and *S. wilsonii* (Horne ex Baker) Becc. have leaf blades that are obviously acute at apex and attenuate at base, and in the latter species the petioles are slender, obvious, and often more than 3 cm. long.

Ixora calcicola A. C. Sm. Bishop Mus. Bull. 220:251, *fig. 13.* 1959.

FULANGA: In thickets on limestone formation, *Smith* 1145 (Bish, GH, UC, US); on lagoon cliff, *Smith* 1219 (Bish, GH, UC, US). ONGEA NDRITI: Rocky sea coast, *Bryan* 387 (A, Bish).

These Lau specimens were taken from shrubs or small trees 1–4 m. high, growing near sea level; the corolla is white, the anthers yellow, and the fruit brown.

Previously I had referred these three specimens to *I. samoensis* A. Gray, which they resemble only superficially; that species has the inflorescence-subtending bracts acute or obtuse to a short-stipitate base, and the calyx obviously pilose. In comparison with the type specimen of *I. calcicola,* from Vava'u, Tonga, the Lau material shows normal variability, having the petioles sometimes up to 1 cm. long, the leaf blades up to 12.5×7 cm., and the corolla with a tube 18–25 mm. long and with lobes perhaps as small as 8×4 mm., somewhat smaller than those described. A more recent collection from Vava'u, *Hotta* 4936 (Bish), differs from the type collection (*Yuncker* 16091) to about the same degree as the Fijian material.

Ixora arestantha A. C. Sm., sp. nov.

Frutex vel arbor 5–12 m. alta, ramulis subteretibus apices versus 2–3 mm. diametro superne pilis pallidis haud 0.1 mm. longis minute puberulis; stipulis subcoriaceis distinctis dorso puberulis 5–7 mm. longis basi late deltoideis in aristam subulatam 3–5 mm. longam angustatis; petiolis saepe inconspicuis interdum manifestis 1–10 mm. longis canaliculatis mox glabratis; foliorum laminis chartaceis in sicco fuscis oblongo-lanceolatis, 9–21 cm. longis, 2.5–7.5 cm. latis, basi anguste rotundatis vel late obtusis, in apicem acutum vel mucronulatum angustatis, supra glabris, subtus (interdum obscure saepe manifeste) pilis 0.05–0.2 mm. longis puberulis, costa supra paullo elevata subtus prominente, nervis secundariis utrinsecus 10–15 patentibus inconspicue anastomosantibus utrinque prominulis vel supra planis, rete venularum inconspicuo laxo utrinque prominulo vel subimmerso; inflorescentiis terminalibus trichotome corymbosis e basi divisis sub anthesi 3–6.5 cm. longis et ad 13 cm. latis, ramulis gracilibus et pedicellis et calyce pilis 0.05–0.2 (–0.3) mm. longis copiose puberulis, bracteis bracteolisque lanceolato-subulatis 0.8–3 mm. longis puberulis; pedicellis gracilibus sub anthesi plerumque 1–3 (–6) mm. longis saepe superne pluribracteolatis; calyce oblongo-cupuliformi sub anthesi 1.7–3 mm. longo et apice 1.2–2 mm. diametro, limbo suberecto hypanthium subaequante conspicue 4-lobato intus obscure strigilloso, lobis oblongo-deltoideis subacutis 0.6–1.5 mm. longis; disco annulari-pulvinato ca. 0.5 mm. diametro; corolla extus obscure puberula vel glabra hypocrateriformi, tubo gracili (0.8–1 mm. diametro) sub anthesi 5–7 mm. longo, lobis 4 patentibus anguste oblongis obtusis 5.5–6 mm. longis 1.5–1.7 mm. latis; staminibus exsertis, filamentis filiformibus 1.5–2 mm. longis, antheris lineari-oblongis 3.5–4 mm. longis utroque acutis ca. 1 mm. supra basim affixis, thecis inferne liberis; stylo gracili 8–9 mm. longo pilis patentibus ca. 0.1 mm. longis setuloso-puberulo superne incrassato, stigmatibus divaricatis 1.3–1.8 mm. longis; fructibus subglobosis 6–7 mm. diametro parce puberulis vel glabris calycis limbo puberulo coronatis.

Type in the U.S. National Herbarium, No. 2191555, collected in dense forest in the hills east of the Wainikoroiluva River, near Namuamua, Namosi Province, Viti Levu, Fiji, alt. 50–200 m., October 15, 1953, by A. C. Smith (No. 8941). Duplicates at Bish, etc.

ADDITIONAL SPECIMENS EXAMINED:

FIJI: VITI LEVU: Serua: Vatutavathe, vicinity of Ngaloa, *Degener* 15199 (A); hills between Wainingggere and Waisese Creeks, between Ngaloa and Wainiyambia, *Smith* 9552 (Bish, US, etc.). Namosi: Hills east of Navua River, *Greenwood* 988 (A). Namosi or Serua: Along stream above waterfall near Namuamua, *Gillespie* 3253 (Bish). Naitasiri: Vicinity of Nasinu, *Gillespie* 3508 (A, Bish, UC, US), 3592 (A, Bish). OVALAU: Hills southeast of Mbureta River, *Smith* 7461 (Bish, US, etc.).

Field notes indicate the plant as a shrub or slender tree 5–12 m. high, occurring at elevations of 50–400 m. in dense forest or dry forest. Color notes of some of the specimens are contradictory, but usually the inflorescence branches and calyx are noted as deep pink to bright red, the corolla tube as greenish to pale pink, and the lobes as deeper pink or dull red (although for No. 9552 I noted the corolla limb as white); the fruit is indicated as red.

In the close indument of the lower surfaces of its leaf blades and of its inflorescence branches and calyx, the new species (of § *Pavettopsis*) suggests *I. pubifolia* A. C. Sm. and *I. greenwoodiana* A. C. Sm., obviously differing from both of these in the rounded or broadly obtuse bases of its leaf blades and its very short petioles. The corollas of *I. arestantha* are substantially smaller than those of *I. pubifolia*, and its calyx lobes are longer than those of either of these species.

A closer relative of the new species may be *I. myrtifolia* A. C. Sm., which has subsessile leaves with the blades rounded or subcordate at base, but that species has the leaves completely glabrous. *Ixora arestantha* further differs from *I. myrtifolia* in the indument (short but obvious) of its inflorescence branches and calyx, in its long-aristate stipules (the awns in *I. myrtifolia* seldom exceeding 2 mm. in length), in the filiform bracts and bracteoles of its inflorescence, and in the obvious and comparatively elongate calyx lobes. The corolla tube of the new species is short and slender for species of this alliance, but comparably mature corollas are not yet known for *I. myrtifolia*.

Ixora prolixa A. C. Sm., sp. nov.

Frutex vel arbor 4–10 m. alta, partibus vegetativis glabris, ramulis subteretibus apices versus 2–4 mm. diametro, internodiis distalibus interdum subcomplanatis et ibi raro obscure puberulis; stipulis subcoriaceis 2–4 mm. longis basi late deltoideis in aristam lanceolatam 1–1.5 mm. longam angustatis; petiolis crassis canaliculatis 11–27 mm. longis; foliorum laminis chartaceis in sicco fusco-olivaceis oblongo-ellipticis, (9–) 12–20 cm. longis, (4–) 5–11 cm. latis, basi rotundatis vel obtusis et in petiolum abrupte decurrentibus, apice obtusis vel subacutis et minute calloso-apiculatis, costa supra leviter depressa vel plana subtus prominente, nervis secundariis utrinsecus 9–12 patentibus marginem versus anastomosantibus utrinque prominulis vel supra planis, rete venularum copioso utrinque plerumque prominulo; inflorescentiis terminalibus trichotome corymbosis amplis e basi divisis sub anthesi 8–23 cm. longis et 11–30 cm. latis, ramulis gracilibus et pedicellis et calyce pilis 0.05–0.2 mm. longis obscure vel manifeste puberulis, bracteis bracteolisque inconspicuis deltoideis

vel lanceolatis acutis 0.5–1 mm. longis mox caducis; pedicellis gracilibus plerumque 3–12 mm. longis (interdum brevioribus) apicem versus obscure bracteolatis; calyce cupuliformi 1.5–2 mm. longo apice 1.2–1.8 mm. diametro, limbo quam hypanthio breviore intus inconspicue strigilloso, lobis 4 late ovato-deltoideis 0.2–0.4 mm. longis rotundatis vel obtusis; disco minuto annulari; corolla glabra vel extus parcissime puberula hypocrateriformi, tubo gracili (0.7–1.3 mm. diametro) sub anthesi 12–20 mm. longo, lobis 4 oblongis obtusis 7–10 mm. longis 2–3 mm. latis; staminibus exsertis, filamentis filiformibus 2–4 mm. longis, antheris lineari-oblongis 7–8 mm. longis 2–2.5 mm. supra basim affixis utroque conspicue angustatis, basi et apice mucronulatis, thecis inferne liberis; stylo gracili exserto breviter setuloso vel subglabro superne incrassato, stigmatibus divaricatis 2–4 mm. longis; fructibus subglobosis 7–10 mm. diametro calycis limbo inconspicuo persistente coronatis.

Type in the herbarium of the Bernice P. Bishop Museum, collected in the central forest of the island of Tuvutha, Fiji, alt. about 100 m., September 11, 1924, by E. H. Bryan, Jr. (No. 548).

ADDITIONAL SPECIMENS EXAMINED:

FIJI: VANUA MBALAVU: Southern limestone section, on the islet Malatta, alt. 0–100 m., *Smith* 1435 (Bish, GH, UC, US). KORO: Eastern slope of main ridge, alt. 300–500 m., *Smith* 969 (Bish, GH, UC, US). NGAU: Slopes of Mt. Ndelaitho, on northern spur, toward Navukailangi, alt. 350–500 m., *Smith* 7879 (Bish, US, etc.).

Field notes indicate the plant as a shrub or tree 5–10 m. high, growing in forest at elevations of near sea level to 500 m. The inflorescence branches and calyx are pink, the corolla white, pinkish at base, the filaments white, and the fruit red or at length brown. The specimens from Koro and Ngau, in fruit, are referred here with reservations, as corollas are required definitely to separate this new species from *I. elegans*; however, in general facies these collections from Loma-i-Viti very closely suggest the two Lauan specimens, each of which bears ample flowering and fruiting inflorescences.

In its strictly glabrous leaves, puberulent inflorescence branches and calyx, and very short calyx limb and lobes, the new species (of § *Pavettopsis*) suggests *I. elegans* Gillespie and *I. decora* A .C. Sm. From *I. elegans*, *I. prolixa* differs in its wide-spreading, larger, more open inflorescence, and especially in its larger flowers, of which the corolla tube is very slender and 12–20 mm. long (rather than 5–6 mm. as in *I. elegans*). In foliage the two species are very similar, but the leaf blades of *I. elegans* are more gradually narrowed to a predominantly acute apex. The related *I. decora* differs from *I. prolixa* in its proportionately narrower leaf blades, more compact inflorescences, and very obscure inflorescence indument.

In the size of its inflorescence and corolla, the new species resembles *I. tubiflora* A. C. Sm. (thus far known only from Taveuni), but that species has obvious, oblong-deltoid calyx lobes, glabrous inflorescence branches, and stipules with a conspicuous (2–5 mm. long) awn.

Psychotria brevicalyx Fosberg, Sargentia 1:132. 1942.

Psychotria gibbsiae var. *velutina* Fosberg, Sargentia 1:127. 1942.

In describing this species, Fosberg cited only fruiting material; he mistook a calycine fragment for an "exceedingly short 5-denticulate calyx-ring" and consequently applied to his concept an inappropriate epithet. Additional material now available indicates that the calyx limb greatly exceeds the hypanthium at anthesis. The relationship of the species is not with *P. turbinata* A. Gray as stated by Fosberg, but rather with *P. pubiflora* (A. Gray) Fosberg and its allies. In this alliance, *P. pubiflora* (which may include *P. crassiflora* Fosberg), *P. gibbsiae* S. Moore, and *P. magnifica* Gillespie all have the lower surface of the leaf blades glabrous. The closest ally of *P. brevicalyx* is *P. nandarivatensis* A. C. Sm., from which it may be distinguished as follows:

Leaf blades 12–24×4–12 cm., copiously hirtellous beneath with pale or reddish hairs usually 0.2–0.5 mm. long, these uniformly distributed and persistent; indument of inflorescence similarly copious and persistent, the hairs 0.5–1.2 mm. long . . . . . **P. brevicalyx**

Leaf blades usually smaller, (5–) 7–16×(2–) 3–6 cm., sporadically hirtellous beneath with reddish hairs 0.5–1 mm. long, these denser on costa and nerves than on surface, rarely essentially lacking; indument of inflorescence similar, often sporadic and rarely essentially lacking . . . . . **P. nandarivatensis**

While the extremes of these two concepts are quite distinct, some specimens are confusingly intermediate. Both species are here retained pending a detailed review of the genus in Fiji. *Psychotria nandarivatensis* is now known from many upland specimens in northern and northwestern Viti Levu.

The type of *P. gibbsiae* var. *velutina* in foliage and indument precisely agrees with material here referred to *P. brevicalyx*, including its type. The inflorescence of the varietal type is comparatively compact, but its calyx is typical for *P. brevicalyx*.

The calyx limb of the concept here accepted as *P. brevicalyx* is quite variable, but is characterized as composed of a cylindrical lower portion 5–10 mm. long and a more or less flaring apical portion. The apex in some specimens is subrotate and 12–15 mm. in diameter, with broad lobes as large as 6×8 mm. Other flowering specimens have the apex only 6–10 mm. in diameter, with oblong lobes 1–5×1.5–2.5 mm. Since foliage and corolla characters are not correlated with these differences, and since the calyx limb itself varies substantially on single plants, I believe this concept of *P. brevicalyx* to be reasonable

for *Psychotria*, in which intraspecific crossing must be locally commonplace. A supplementary description of the inflorescence follows:

Inflorescence branches, pedicels, and calyx copiously hirtellous, the indument composed of pale, many-celled spreading hairs 0.5–1.2 mm. long; calyx 10–15 (rarely to 20) mm. long, the hypanthium cupuliform, about 2 mm. long, the calyx limb ascending in a cylindrical tube 5–10 mm. long and 3.5–4 mm. in diameter, broadening or flaring into an apical portion 6–15 mm. in diameter, this conspicuously or obscurely reticulate-veined, pilose without and less obviously so or glabrous within, the lobes 5, variable, broadly deltoid to oblong, 1–6 mm. long, 1.5–8 mm. broad, obtuse at apex, the sinuses obtuse or subacute; corolla cylindric, gradually broadened distally, 18–20 mm. long, copiously hirtellous without with pale few- or several-celled hairs 0.2–1 mm. long, the tube puberulent or tomentellous within distally, the lobes oblong, 4–5 mm. long, about 1.5 mm. broad, subacute, obscurely puberulent within; filaments slender, 2–4 mm. long, appressed to corolla throat and similarly pilose, the anthers oblong, 2–3 mm. long, obtuse at both ends; style filiform, about as long as the corolla, the stigmas recurved, about 1 mm. long.

The species is known from the two large islands of Fiji, at elevations of near sea level to 600 m. (the Gillespie specimen is said to be from Mt. Naitarandamu at about 1,150 m.). Following are the specimens referable to it, cited without details except for the island and province:

VITI LEVU: Nandronga & Navosa: *Degener* 15256, 15292 (type US; Yawe, vicinity of Mbelo, near Vatukarasa, alt. 120–300 m.), *Tabualewa* 15620. Serua: *Tabualewa* 15605 (US, type of *P. gibbsiae* var. *velutina*; Mbuyombuyo, near Namboutini), *Degener* 15154, *Smith* 8997, 9206, 9656. Namosi: *Gillespie* 3131, Smith 8726, 8893, 8898. VANUA LEVU: Thakaundrove: *Smith* 1856.

Psychotria stenantha A. C. Sm., sp. nov.

Frutex vel arbor parva 4–5 m. alta ubique praeter pilos obscuros inter stipulas et inflorescentiae bracteolis et calycis margine glabra; stipulis 6–12 mm. longis inferne connatis superne liberis et late bifidis; petiolis gracilibus 7–15 mm. longis, foliorum laminis subcoriaceis in sicco fuscis et copiose immerso-glandulosis, elliptico-oblongis, 7–10 cm. longis, 2.5–5 cm. latis, basi acutis, apice obtusis vel obtuse cuspidatis, margine anguste recurvatis, costa utrinque prominente, nervis secundariis utrinsecus 10–12 patentibus supra subplanis subtus elevatis, rete venularum subimmerso; inflorescentia compacta ad 2 cm. diametro e basi 3- vel 4-divisa, ramulis 2- vel 3-plo divisis, floribus plerumque trinis, bracteolis sub floribus minutis saepe crispato-pilosis (pilis 0.2–0.5 mm. longis), pedicellis teretibus 1–2 mm. longis; calyce cylindrico 3–3.5 mm. longo (hypanthio obconico ad 1 mm. longo incluso), limbo ca. 1.5 mm. diametro apice abrupte sed

inconspicue ad 2 mm. patente et ibi pilis brunneis pluricellularibus 0.1–0.2 mm. longis inconspicue ciliolato 4- vel 5-denticulato, dentibus deltoideis acutis haud 0.3 mm. longis, sinibus rotundatis; corolla carnosa in alabastro ad 5 mm. longa intus faucibus pilosa, lobis 4 vel 5 obtusis; staminibus 4 vel 5, filamentis in alabastro brevibus, antheris oblongis 1.7–2 mm. longis utroque obtusis; disco minuto glabro; stylo gracili apice bifido.

Type in the herbarium of the Arnold Arboretum, collected in thick forest on the Mt. Evans Range, Mba Province, Viti Levu, Fiji, alt. about 1,050 m., September 24, 1944, by William Greenwood (No. 1062A). Duplicate at Bish.

In its narrow, erect calyx limb obviously exceeding the hypanthium in length, and in its glabrous habit, *P. stenantha* is closely related only to *P. vitiensis* Fosberg (*Calycosia monticola* Gillespie) and *P. mundula* A. C. Sm. From the former it differs obviously in its comparatively short calyx limb (2–2.5 mm. long instead of 4.5–7 mm.), and also in its somewhat larger leaves with more numerous, spreading secondaries. The corolla of the type collection is too young to permit comparison. From *P. mundula* the new species differs in its comparatively open habit, larger leaves, more open inflorescence, and short calyx lobes.

Psychotria hemisphaerica Gillespie, Bishop Mus. Bull. 91:32, *fig. 35*. 1932.

In discussing *P. carnea* (Forst. f.) A. C. Sm. (Bishop Mus. Bull. 141:151. 1936), based on *Petesia carnea* Forst. f., I placed *P. hemisphaerica* in its synonymy. Upon further examination of the Fijian material now available, I believe Gillespie's concept to merit specific recognition. It is readily distinguished from *P. carnea* by having the distal branches of its inflorescence, its pedicels, bracts, and calyx puberulent (with pale hairs that are minute but apparent, 0.05–0.1 mm. long). The indument extends to both surfaces of the calyx limb and is usually, but not always, persistent in fruit. The corresponding parts of *P. carnea* are glabrous.

Gillespie did not cite a type, and this becomes a matter of consequence because the 17 specimens cited by him are, in my opinion, referable to four species. The following collections represent *P. carnea*: *Gillespie* 2975.1, 3300, *Parks* 20226, 20265, 20465. *Gillespie* 3793 represents *P. incompta* A. C. Sm., and *Gillespie* 2353 *P. pittosporifolia* Fosberg.

An exchange of correspondence between Gillespie and Miss Marie C. Neal (then in charge of the Bishop Museum herbarium) is pertinent in the designation of a lectotype for *P. hemisphaerica*. In this, Gillespie asked Miss Neal to select a specimen most resembling his figure 35; she has indicated *Gillespie* 2208, which indeed seems to be the basis for the habit drawing and the fruit (figs. *b*, *c*). I believe that *Gillespie* 4592 must have served as the basis for the flower

drawings (figs. *a*, *d*, *e*). As the lectotype for this concept, *Gillespie* 2208 in the Bishop Museum herbarium may be accepted.

Psychotria hemisphaerica is known only from the islands of Viti Levu and Vanua Levu, with a single specimen from Ongea Levu in Lau, at elevations from near sea level to about 600 m. Following are the specimens referable to it, cited without details except for the island and province:

VITI LEVU: Nandronga & Navosa: *Smith* 4713. Serua: *Degener & Ordonez* 13622, *Tabualewa* 15581, *Smith* 9236, 9363. Namosi: *Greenwood* 1041. Naitasiri: *Gillespie* 2457, 3425, 3467, 3519, *Setchell & Parks* 15098, 15167, *Parks* 20069, *MacDaniels* 1146, *B. E. Parham* 974, *Degener & Ordonez* 13763. Rewa: *Gillespie* 2208 (lectotype Bish; southeastern slopes of Mt. Korombamba, alt. 400 m.), 2260, 4592, *Parks* 20121, 20315, *Meebold* 16876, 17043. VANUA LEVU: Mathuata: *Smith* 6420. Thakaundrove: *Smith* 588. ONGEA LEVU: *Bryan* 422. Fiji, without locality: *Horne* 705.

Psychotria hemisphaerica is one of a group of five interrelated Fijian species, the others being *P. carnea* (which also occurs in Samoa and Tonga), *P. hunteri* (Horne ex Baker) A. C. Sm., *P. archboldiana* Fosberg, and *P. incompta*. This group, which scarcely merits my previous designation as *Psychotria* sect. *Eumachia* (DC.) A. C. Sm. (Bishop Mus. Bull. 141:151. 1936), is characterized as follows: Calyx limb suberect or erecto-patent, 2–5 mm. long, often thin and obviously nerved, and fairly persistent in fruit; corolla limb sharply enlarged and 4-angled or 4-winged just prior to anthesis, the corolla lobes broad and obviously veined, appressed at their inner margins to form the angles or wings; stipular and pyrene characters are also reasonably constant but are duplicated in other species groups, and a consideration of their value must await revision of all the Fijian *Psychotriae*. The species of this alliance are not always sharply demarcated, and *P. hemisphaerica* may be expected to intergrade with *P. carnea* and *P. archboldiana*. Students of *Psychotria* (among innumerable other insular genera) must be reconciled to the plastic nature of their concepts, which cannot be discarded merely because occasional individuals demonstrate intermediate characteristics.

Psychotria scitula A. C. Sm., sp. nov.

Arbor parva ut videtur; ramulis gracilibus cinereis glabris internodiis ultimis paullo complanatis; stipulis in vaginam subcoriaceam gracilem valde connatis, vagina cylindrica superne gradatim contracta 6–12 mm. longa pilis rubiginosis multicellularibus 0.5–1 mm. longis hirtella demum glabrata, stipularum apicibus liberis lanceolato-subulatis inconspicuis 1–2 mm. longis; petiolis gracilibus 10–25 mm. longis, laminis foliorum praeter costam subtus ut stipulis rubiginoso-hirtellam glabris papyraceis in sicco fuscis, obovato-lanceolatis, 9–16 cm. longis, 3–6 cm. latis, basi acutis et in petiolum longe decurrentibus,

in acuminem conspicuum gracilem 1–2 cm. longum gradatim angustatis, supra cystolithis linearibus inconspicue ornatis, costa supra elevata subtus prominente, nervis secundariis utrinsecus 11–16 arcuato-adscendentibus marginem versus manifeste anastomosantibus supra subplanis subtus elevatis, rete venularum laxo supra immerso subtus prominulo; inflorescentia laxa e basi 5-ramulosa, ramulis 3.5–6 cm. longis gracilibus debilibus glabris superne trichotome divisis, bracteolis sub floribus oblongo-linearibus 1–3 mm. longis 0.2–1 mm. latis extus copiose vel sparse strigillosis (pilis ut eis calycis), floribus plerumque trinis sessilibus; calyce anguste cupuliformi sub anthesi 3–3.5 mm. longo et apice 2–2.5 mm. diametro extus basi excepta pilis rubiginosis 0.4–1 mm. longis plerumque 5–7-cellularibus copiose hirtello, hypanthio parvo obconico, limbo erecto submembranaceo inconspicue glanduloso-ornato intus glabro 2–2.5 mm. longo subtruncato, dentibus 5 minutis; corolla cylindrica ad 5 mm. longa (immatura) utrinque glabra vel pilis paucis apicalibus inconspicue ornata, lobis 5 oblongis 1.5–2 mm. longis obtusis; staminibus 5, filamentis brevibus glabris, antheris oblongis ca. 2 mm. longis utroque obtusis; disco annulari-pulvinato glabro; stylo in alabastro corollam subaequante apice bifido.

Type in the herbarium of the B. P. Bishop Museum, collected on Mt. Voma, Namosi Province, Viti Levu, Fiji, alt. 900 m., September 6, 1927, by John W. Gillespie (No. 2789). Duplicates at GH, UC. Another collection from the same locality, alt. 800 m., is *Gillespie* 2672 (A, Bish, GH, UC).

Psychotria scitula is closely allied only to *P. filipes* A. Gray and *P. diffusiflora* A. C. Sm., differing from both in its sessile flowers, the striking indument of its calyx, and its comparatively elongate calyx limb. Both of the older species have pedicellate flowers with the calyx limb glabrous and 0.5–1 mm. long. *Psychotria diffusiflora* further has the corolla copiously barbellate within, while that of *P. filipes* is essentially glabrous within. Now that more adequate material is at hand, the difference in leaf shape between *P. filipes* and *P. diffusiflora* is less significant than I previously thought, but in this respect the new species more closely resembles typical *P. diffusiflora.* Another species of this relationship, *P. pelagica* Seem., is in my opinion questionably separable from *P. filipes.*

In connection with the new species, *P. vomensis* Gillespie should be mentioned; as the name implies, this also occurs on Mt. Voma. Both species have the flowers in sessile triads and the calyx copiously pilose. However, *P. vomensis* has the inflorescence comparatively compact, each inflorescence ray being usually unbranched and obviously pilose; the calyx indument is composed of usually unicellular pale hairs scarcely 0.1 mm. long; the calyx limb is subspreading and with obvious lobes; the leaf blades are proportionately broader and obtuse to obtusely short-cuspidate at apex, and lack the costal indument;

and the stipules are of quite a different type, being free and deeply bifid in the distal half.

Psychotria consobrina A. C. Sm., sp. nov.

Arbor gracilis vel frutex 3–5 m. altus, ramulis gracilibus internodiis distalibus copiose sed minute papilloso-puberulis (pilis unicellularibus); stipulis 8–10 mm. longis extus copiose puberulis inferne connatis superne in lobos 3–5 mm. longos et 0.8–1.5 mm. latos apice acutos vel attenuatos bifidis; petiolis gracilibus semiteretibus 1.2–5 cm. longis primo puberulis demum glabratis, laminis foliorum chartaceis in sicco fuscis ellipticis vel lanceolato-ellipticis, (9–) 10–20 cm. longis, (2–) 4–7.5 cm. latis, basi acutis et in petiolum decurrentibus, apice acuminatis (acumine ad 1 cm. longo) vel obtuse cuspidatis, obscure immerso-glandulosis, utrinque glabris, costa supra subplana subtus prominente, nervis secundariis utrinsecus 12–18 patentibus curvatis marginem versus anastomosantibus supra subplanis subtus elevatis, rete venularum intricato utrinque subimmerso vel subtus prominulo; inflorescentia ampla cymosa 5–12 cm. longa 4–10 cm. lata manifeste pedunculata 3- vel 4-plo divisa, axibus pedicellisque gracilibus copiose puberulis (pilis pallidis 1–3-cellularibus 0.05–0.1 mm. longis), pedunculo 2–7 cm. longo valde reflexo, bracteis lanceolato-subulatis 1.5–3.5 mm. longis utrinque puberulis plerumque trifidis, lobo centrali longissimo, bracteolis sub floribus similibus sed 1–2 mm. longis; floribus plerumque trinis, pedicellis sub anthesi 1–5 mm. longis, calyce et corolla minute sed copiose puberulis (pilis plerumque unicellularibus); hypanthio cupuliformi sub anthesi haud 1 mm. longo, calycis limbo erecto-patente 1.5–2 mm. longo et apice 2.5–3.5 mm. diametro copiose immerso-glanduloso intus puberulo, lobis 5 semiorbicularibus 0.5–1 mm. longis et 1.5 mm. latis; corolla cylindrica sub anthesi 9–10 (–13) mm. longa superne paullo ampliata intus medium versus pilis pallidis multicellularibus 0.5–0.8 mm. longis copiose tomentello-barbata, lobis 5 oblongis 2–3 mm. longis obtusis intus cucullatis; staminibus 5, filamentis glabris 1.5–2 mm. longis, antheris oblongis ca. 2 mm. longis utroque obtusis; disco annulari-pulvinato ad 0.8 mm. alto et 1.3 mm. diametro; stylo corollam subaequante superne papilloso apice bifido; fructibus obovoideo-ellipsoideis demum glabratis in vivo carnosis in sicco inconspicue angulatis, 8–9 mm. longis, 5–7 mm. latis, calycis limbo manifeste puberulo coronatis, pyrenis semi-obovoideis 6–7×4–6×2–3 mm., ventre complanatis, dorso obtuse et inconspicue 3- vel 5-carinatis.

Type in the herbarium of the B. P. Bishop Museum, collected in limestone hills near quarry beyond Lami village, Rewa Province, Viti Levu, Fiji, alt. 50 m., February 6, 1928, by John W. Gillespie (No. 4596). Duplicates at GH, UC.

ADDITIONAL SPECIMENS EXAMINED:

FIJI: VITI LEVU: Nandronga & Navosa: Vicinity of Mbelo, near Vatukarasa, *Degener* 15292a (A), *Tabualewa* 15623 (A, Bish, UC, US). Serua: North of Korovou, *St. John* 18933 (Bish, GH); hills west of Waivunu Creek, between Ngaloa and Korovou, *Smith* 9300 (Bish, US, etc.); hills north of Ngaloa, in drainage of Waininggere Creek, *Smith* 9157 (Bish, US, etc.); hills between Waininggere and Waisese Creeks, between Ngaloa and Wainiyambia, *Smith* 9383 (Bish, US, etc.). Namosi or Serua: Vicinity of Namuamua, *Gillespie* 2996 (A, Bish, UC, US). Ra: Vicinity of Rewasa, near Vaileka, *Degener* 15335 (A, Bish, UC, US), 15380 (A), 15449 (A, US), 15525 (A, US). These specimens occur from near sea level to about 300 m., in dense wet or dry forest; the corolla is reported as white and the fruit as red.

The complex of forms related to *P. furcans* Fosberg is difficult to understand on the basis of available material, but I believe that my discussion in Journ. Arnold Arb. 34:105 (1953) requires amending. The closest relative of *P. furcans* appears to be *P. pritchardii* Seem., with which it has in common a spreading, obviously pedunculate, and usually reflexed inflorescence. From *P. pritchardii*, *P. furcans* and the new species here discussed differ in having the stipules comparatively small, not auriculate, with the free portion bifid into acute lobes, and the inflorescence peduncle comparatively short, 2–7 cm. long. *Psychotria pritchardii* has extraordinary, auriculate stipules, interconnected by a flange of tissue proximal of each petiole, the free portion being bifid into broad, rounded lobes, and the peduncle greatly elongated, 7–35 cm. long. On the basis of available specimens, *P. pritchardii* seems limited to Taveuni and Vanua Levu.

The new species, as represented by the specimens cited above, differs from typical *P. furcans* in the copious but minute indument of its young parts, stipules, inflorescence peduncle and branchlets, pedicels, calyx, and corolla; further its calyx limb is longer and more spreading, with larger, rounded lobes, its pyrenes are obtusely 3- or 5-carinate rather than with a prominent, thin, median dorsal keel, and its leaf blades are prevailingly elliptic rather than oblong-lanceolate. In addition to typical *P. furcans*, from upland Viti Levu, and typical *P. consobrina*, from lowland Viti Levu, there is available a series of confusing specimens, mostly from upland Viti Levu, that show relationships to both concepts. Because these specimens have the puberulent inflorescence parts (including calyx and corolla) and the comparatively large calyx limb of *P. consobrina*, I believe this to be their better position. But they have, in general, the oblong leaf-blades, glabrous young parts, and glabrous stipules of typical *P. furcans*. The calyx tube, in some of these specimens, is as much as 3 mm. long and in shape suggestive of that of *P. chrysophylla* Fosberg, a species with a more pronounced inflorescence indument of several-

celled, longer, reddish hairs. These questionable specimens, now referred to *P. consobrina* with reservations, are:

VITI LEVU: Mba: *Gillespie* 3695, *Parks* 20537, 20680, *Degener* 14369, 14525, 14625, 14637, 14658, 14746, *Greenwood* 889, 889A, 1163, 1246, 1250, *Smith* 4091, 4277, 4354, 4372, 5980, 6038, 6270. NANDRONGA & NAVOSA: *Smith* 5411, 5477, 5608. MOTURIKI: *Seemann* 244. VANUA LEVU: Mathuata: *Smith* 6671, 6824.

While a complex of morphological intermediates among these three species—*P. furcans*, *P. consobrina*, and *P. chrysophylla*—may be expected to occur, the extremes seem to have a degree of individuality that makes their recognition as species desirable.

In connection with the above citation of *Seemann* 244, it should be noted that this was one of the two collections originally cited by Seemann as representing his *P. broweri* (Seem. Fl. Vit. 135. 1866). These two collections are not conspecific, although both came from the island of Moturiki. The second, *Seemann* 254, was informally chosen as the lectotype by Gillespie, as I indicated in Journ. Arnold Arb. 34:104. 1953. Such a choice is herewith formalized, since it has been followed in herbaria, where *P. broweri* is now well represented by material from several islands of Fiji. It is an essentially glabrous plant, characterized by having its inflorescence epedunculate, with 3–6 branches from the base; its relationship is with *P. platycocca* A. Gray and *P. filipes* A. Gray.

Psychotria salticola A. C. Sm., sp. nov.

Arbor vel frutex 4–8 m. altus inflorescentia excepta glaber, ramulis subteretibus internodiis distalibus subcomplanatis; stipulis conspicuis papyraceis ellipticis, eis inflorescentiam juvenilem obtegentibus ad 3 cm. longis et 1.5 cm. latis in vaginam latam inferne connatis, superne liberis manifeste nervatis conspicue bifidis, lobis oblongo-deltoideis 4–8 mm. longis latisque apice obtusis; petiolis gracilibus semiteretibus 2–4 cm. longis, laminis foliorum chartaceis in sicco fusco-viridibus copiose glanduloso-punctatis, anguste ellipticis, (12–) 15–24 cm. longis, (3.5–) 5.5–10 cm. latis, basi acutis et in petiolum longe decurrentibus, apice in acuminem brevem ad 1 cm. longum obtuse cuspidatis, costa supra elevata subtus prominente, nervis secundariis utrinsecus 11–14 erecto-patentibus arcuatis supra subplanis subtus valde elevatis, rete venularum subimmerso vel subtus subprominulo; inflorescentia terminali compacta multiflora e basi 3–5-divisa sub anthesi ad 4 cm. longa, ramulis gracilibus 2- vel 3-plo divisis et pedicellis hirtellis (pilis pallidis vel rubiginosis patentibus 0.1–0.2 mm. longis 2–4-cellularibus), bracteis bracteolisque inconspicuis oblongo-lanceolatis 0.5–1 mm. longis superne fimbriatis; floribus plerumque trinis, pedicellis gracilibus sub anthesi 2–4 mm. longis interdum glabris; calyce anguste cupuliformi vel subfusiformi sub anthesi 3.5–5 mm. longo,

hypanthio obconico 1–1.5 mm. longo parce hirtello vel glabro, limbo erecto subcarnoso 2.5–3.5 mm. longo apice 2.5–3 mm. diametro utrinque glabro margine pilis ut eis pedicelli conspicue fimbriato, 4–6-denticulato vel lobato, lobis minutis vel interdum semiorbicularibus ad 0.5 mm. longis; corolla subcarnosa cylindrico-infundibuliformi sub anthesi ad 12 mm. longa, extus copiose (vel tantum apice) pilis 0.1–0.3 mm. longis 2–5-cellularibus hirtella, intus medium versus pilis brevioribus saepe unicellularibus barbellata, lobis 4–6 oblongis 2–2.5 mm. longis obtusis; staminibus 4–6, filamentis minutis, antheris oblongis 1.6–1.8 mm. longis utroque obtusis; disco annulari-pulvinato glabro ad 0.8 mm. alto; stylo gracili corollam subaequante apice bifido; inflorescentiae ramulis sub fructu ad 6 cm. longis et pedicellis ad 12 mm. longis, fructibus juvenilibus ellipsoideis calycis limbo erecto coronatis.

Type in the U.S. National Herbarium, Nos. 2191239 and 2191240, collected in dense forest in the hills bordering Wainavindrau Creek, in the vicinity of Wainimakutu, Namosi Province, Viti Levu, Fiji, alt. 150–250 m., September 17, 1953, by A. C. Smith (No. 8550). Duplicates at Bish, etc.

ADDITIONAL SPECIMENS EXAMINED:

FIJI: VITI LEVU: Namosi: Hills north of Wainavindrau Creek, between Korombasambasanga Range and Mt. Naitarandamu, alt. 250–450 m., *Smith* 8491 (Bish, US, etc.).

Field notes indicate the plant as a tree or shrub 4–8 m. high, with the inflorescence branches, pedicels, and calyx pink or dull pink and the corolla white. The two collections here referred are not identical, but they agree so closely that they must be considered conspecific; the above description is inclusive. The type has the inflorescence parts obviously pilose, whereas No. 8491 has the inflorescence branches and pedicels only sparingly so and the corolla (in young bud) glabrous except at apex; the latter collection also has the calyx limb with obvious lobes, whereas that of the type is only minutely denticulate.

The new species is most closely allied to *P. brackenridgei* A. Gray, a fairly variable species that is known from many collections and several islands, with which it has in common large, glabrous, prevailingly elliptic leaf blades, bifid stipules with broad, obtuse lobes, an inflorescence branching from the base, and a fairly obvious inflorescence indument composed of several-celled, often reddish hairs. *Psychotria brackenridgei*, however, has the calyx limb erecto-patent, comparatively short (seldom exceeding 1 mm. in length), and copiously pilose on both sides, whereas in *P. salticola* the calyx limb is erect, longer (2.5–3.5 mm. long), and glabrous except for the fimbriate margin. In general aspect *P. salticola* also suggests *P. broweri* Seem., but that species has a strictly glabrous inflorescence and a short calyx limb (0.5–0.8 mm. long).

Compositae

Crassocephalum crepidioides (Benth.) S. Moore, Journ. Bot. 50:211. 1912.

VITI LEVU: Namosi: Northern base of Korombasambasanga Range, in drainage of Wainavindrau Creek, *Smith* 8669 (Bish, US, etc.); hills east of Wainikoroiluva River, near Namuamua, *Smith* 9069 (Bish, US, etc.). OVALAU: Valley of Mbureta and Lovoni Rivers, *Smith* 7393 (Bish, US, etc.).

The cited specimens are from coarse or succulent herbs up to 1 m. high, naturalized along streams and on open gravel banks and rocky shores of rivers at altitudes of 20–400 m.; the florets and stigmas are dull yellow, distally tinged with bright or reddish orange.

Crassocephalum crepidioides is now widely distributed from Africa to southern Asia and the Philippines; it extends in the Pacific eastward at least to New Guinea and Ponape, but apparently it has not been previously recorded from Fiji. Belcher (Ann. Mo. Bot. Gard. 43:13. 1956) has commented on the fact that in herbaria this weed is often confused with *Erechtites hieracifolia* (L.) Raf. ex DC.

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THE GENUS CYRTANDRA IN FIJI

By GEORGE W. GILLETT

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THE GENUS CYRTANDRA IN FIJI [1]

GEORGE W. GILLETT

Introduction

The present study is a limited revision of the genus *Cyrtandra* in Fiji and is related to the series initiated by A.C. Smith on selected families of phanerogams from Fiji and the adjacent archipelagos. The earlier work on *Cyrtandra* in Fiji (Seemann, 1861, 1866; Gray, 1862; Clarke, 1883; Gillespie, 1930; Smith, 1936, 1942, 1953) necessarily emphasized exploration and the description of new species. This preliminary phase has included well over 200 collections and the description of a total of 45 species. The present work emphasizes the review of previously known species, the amplification of early descriptions, and a comparative study to provide for the delineation of infrageneric groups and the identification of species.

The importance of *Cyrtandra* in Fiji was emphasized by Smith (1953) who noted that it was exceeded in number of species only by *Psychotria*. The wide distribution and frequent occurrence of this Malaysian-Pacific genus make it an important element in several other floras, including that of Polynesia. Therefore, the present study included a review of all Polynesian species and an investigation of relationships between the Cyrtandrae of Fiji and those of Polynesia.

In number of species (ca. 600) *Cyrtandra* is the largest genus in the Gesneriaceae, and among the families of Engler's Tubiflorae (including the Polemoniales, Lamiales, and Scrophulariales) it is exceeded in number of species only by the genus *Solanum*. Its territory extends from Malaya to Eastern Polynesia, with centers of diversity in Borneo and New Guinea. B. L. Burtt (written communication) estimates the number of species to be between 130 and 150 for each of these centers. The great diversity and the large number of species in the genus impose formidable demands on the taxonomist who aspires to interpret its infrageneric taxonomy. Notable among those who have

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attempted this was C. B. Clarke who, in 1883, described 2 subgenera and 13 sections based on a study of 167 species. In 1888, Hillebrand described five sections, these embracing only the species indigenous to the Hawaiian Islands. Schlechter (1923) published a treatment of the *Cyrtandra* of New Guinea in which he recognized 96 species, dividing these among two subgenera and 14 sections. Unlike his predecessors, Schlechter provided a key to his sections. His treatment probably has considerable merit, yet it pertains to only a portion of the genus, and surely excludes significant evolutionary lines among the hundreds of species that do not occur in New Guinea. It is because of the incomplete, questionable status of the present infrageneric taxonomy that I have not followed any one interpretation but instead have designated provisional species groups that appear as homogeneous, natural units. None of these are formally described and named because certain groups include species outside of Fiji, and these will require revisions as future work is accomplished. Through successive regional treatments of this type, perhaps the infrageneric relationships can gradually be brought into focus and the principal evolutionary stocks described and named with the minimum of ambiguity and confusion.

Smith (1955) has shown that many genera in the flora of Fiji have their maximum speciation in territory to the west, principally in New Guinea, with a poorer representation in Fiji. This attenuated phytogeographic pattern is expressed by *Cyrtandra*, which has approximately 250–300 species in New Guinea and Borneo but only 35 species in Fiji by the present treatment. Further exploration will surely increase the number of species in Fiji, but the possibility of the adjusted figure being more than a relatively small fraction of the total for New Guinea and Borneo seems most unlikely. The examination of extensive herbarium material representing all of Polynesia, but of only limited material from New Guinea, Borneo, and the Philippines, suggests that the Fijian and Polynesian species combined portray only a subsidiary portion of the total morphological expression for the genus.

A short summary of the phytogeographical relationships of the six species groups that are recognized in this paper is in order. Each of these is further discussed under the particular species. Species Group 1 (the *Cyrtandra vitiensis* group) extends from Fiji to Samoa and Hawaii. Species Group 2 (the *C. chippendalei* group) extends from Fiji to Samoa, southern Polynesia, and Hawaii. Species Group 3 (the *C. kandavuensis-C. attenuata* group) extends eastward from Fiji, occurring throughout most of Polynesia. Species Group 4 (the *C. denhamii* group) extends eastward from Fiji to Samoa and the Marquesas Islands but is not known in Hawaii. Neither Group 5 (the *C. harveyi* group) nor Group 6 (the *C. prattii* group) are known to occur east of

Fiji. However, both Group 5 and Group 6 have closely related species in New Guinea, verified by the comparison of herbarium material.

In his recent monograph of *Cyrtandra* on Oahu, Hawaiian Islands, St. John (1966) recognizes a total of 133 species, an amazing concentration for an island of only 600 square miles, of which only a small portion is *Cyrtandra* territory. However, a herbarium and field study of the Oahu species and of the other Hawaiian species reveals that they are relatively homogeneous in comparison with the Fijian Cyrtandrae. Using the key to the six species groups in Fiji, all of the Hawaiian species would be accommodated in Group 1, Group 2, and Group 3. Remarkable similarities exist between Group 2 (the *C. chippendalei* group) and subgenus *Brachycyathus* in St. John's monograph. However, the former embraces only 8 species for all of Fiji, while the latter includes 4 sections and 89 species for the island of Oahu.

Habitat Relationships

Guppy (1906) indicated that the Cyrtandrae of the Pacific Islands are most frequent in moist woods among rank vegetation, but he also stated that they may occur in more exposed and drier habitats. Field observations that I made in Java, Borneo, and Hawaii indicate that *Cyrtandra* invariably grows as an understory element in dense rain forest, often in ravines and gorges characterized by high humidity, very low light intensities, and an almost constant moisture supply. In many species the root systems are shallow, often clinging to the surfaces of moist rocks. These habitat characteristics pertain to elevations between 50 and 2,000 meters. It is known that some species of *Cyrtandra* are capable of surviving intermittent droughts, but in the Pacific the genus is in no instance adapted to arid or semiarid, exposed habitats. The basic relationship is with upland rain forests, and the genus occurs only on the islands of the Pacific where substantial areas of upland rain forest are preserved. It is not an element of the strand flora, and it does not occur on "high" islands that have a low rainfall. Examples of the latter include Niihau, in the Hawaiian Islands, from which no *Cyrtandra* collections are known, even though populations abound on the island of Kauai, scarcely 20 miles distant. It is not likely that *Cyrtandra* could have established founder populations on Pacific islands prior to the development of a relatively dense overstory vegetation. Considering the large number of species in the genus and its extensive geographical range, it would appear to have an unusually narrow habitat relationship. The habitats in Hawaii seem remarkably uniform in character to the point of making it very difficult to cite differences that could account for the presence of a given species in one area and its exclusion from another.

Pollination and Breeding System

The consideration of the breeding system and its relationship to variability and the delineation of species should precede a taxonomic study, if possible. This information provides helpful guidelines for the interpretation of variability and morphological differences within and between populations. The types of variation patterns to be expected from different breeding systems have been presented by Baker (1959), whose interpretations are followed in this study. It has not been possible to carry out a field study of *Cyrtandra* in Fiji, but this has been accomplished on populations of closely related species in Hawaii—plants that have the same basic floral morphology, and the white, fleshy corollas that characterize at least three-fourths of the species known in Fiji. The observations cited below have been made by me on several Hawaiian species occurring on Kauai, Oahu, Lanai, Molokai, Maui, and Hawaii, and together they present a consistent pattern of floral ontogeny and pollination.

The flowers of *Cyrtandra* are protandrous, and there appears to be a conspicuous provision for outcrossing. This is promoted not only by the earlier maturity of the anthers but also through the positioning of the anthers and stigma to minimize self-pollination. The effectiveness of this system is indicated by the complete absence of fruit in 116 bagged flowers of the Oahu species, *Cyrtandra garnotiana* Gaud., and by the production of fruit in 39 out of 42 unbagged controls on the same plants. Self-incompatibility is not known in the Gesneriaceae, and the above evidence is most inadequate for postulating its occurrence in *Cyrtandra*. Therefore, a measure of inbreeding remains a possibility inasmuch as the complete exclusion of entomophilous self-pollination would seem unlikely.

At early anthesis, the filaments extend forward in the corolla tube and hold the basifixed, apically coherent anthers with the connectives against the wall of the tube and the thecae face-to-face on the midplane of the tube. The anthers are then parted from below and are spread so that the thecae lie in one plane. Simultaneously, the anthers are elevated so that the connectives are appressed to the tube opposite the upper sinus. The thecae now occupy a position directly over the access to the nectiferous, cupulate annular disc at the base of the tube. At this time the immature lobes of the stigma are closely appressed. In later anthesis the anthers are shifted in position, being lowered to the anterior surface of the tube, the thecae appressed to the tube opposite the lower lobe, so that any residual pollen is isolated from contact with the mature stigma. The stigmatic lobes now expand and separate, the cleft of separation usually extending farther down on the anterior side of the style, so that the lobes very often form a

cordate receptive surface. The extended stigma is now held over the access to the nectary, near the position formerly occupied by the thecae of the anthers. It is clear that two patterns of configuration are displayed by a given flower and that two insect visits are necessary for accomplishing cross-pollination. Actual pollination has not been observed, but it is assumed that this is accomplished by night-flying Lepidoptera attracted to the white corollas and inflorescences. A lepidopterous antenna has been recovered from one flower. These observations confirm earlier reports of protandry in *Cyrtandra* by St. John (1966) and Carlquist (1965, 1966).

In at least one Fijian species, *Cyrtandra harveyi*, the outbreeding system is further specialized through the gynodioecious habit, and unisexual flowers are known to occur in several additional species in New Guinea and the Pacific.

It seems clear that in Pacific species of *Cyrtandra* there is a very strong trend to outcrossing which in turn would promote variability involving many genotypes (Baker, 1959). The outcrossing mechanism would be expected to facilitate interspecific cross-pollinations since flowers of different species often are remarkably similar, and two, three, or more species very often occur in the same relatively narrow habitat. One putative interspecific hybrid, between *C. milnei* and *C. vitiensis*, has been distinguished in the present study.

The outcrossing breeding system provides for the retention of temporarily disadvantageous genes, including new mutations, through their inclusion in heterozygous genotypes. Such a breeding system would thus tend to enlarge the genetic resources, providing for flexibility. It is significant that this system is, in *Cyrtandra*, correlated with the propensity of the genus to establish populations on isolated island habitats. This breeding system, through its provision of maximum genetic resources for the immigrants and of maximum flexibility for the founder population, is probably of considerable significance in the successful establishment of populations on island habitats.

The recombination potential of a species is increased by its capacity for the dispersal of diaspores (Grant, 1958). In the Pacific species of *Cyrtandra*, the fruit is nearly always a conspicuous, succulent berry, and there seems little reason to doubt the thesis of Guppy (1906) that these are eaten and dispersed by birds. The seeds are very small, usually less than 1 mm. in diameter, with perhaps 50 to 100, or more, per fruit. The seed dispersal would seem to be very effective, so that a given population could include progeny of neighboring populations that lie beyond the range of pollen vectors. This would suggest that the variability of a given species would be a pattern of intergradations extending over a territory of generous dimensions. However, inter-island dispersal apparently is not common in *Cyrtandra*, for a great

many species are restricted to a single island, and few species are known to occur beyond a given archipelago (Guppy, 1906). This restriction is indicated in the Fijian species (fig. 1, table 1).

The extensive geographical territory and impressive speciation of *Cyrtandra* suggest that an effective balance is maintained between dispersal and geographical isolation. The genus has had dispersability sufficient to accomplish its distribution over the vast expanses of the western Pacific. However, the high level of speciation suggests that there have been time intervals between dispersal events, and that these have been of duration sufficient to provide the geographical isolation requisite for evolutionary change.

Acknowledgments

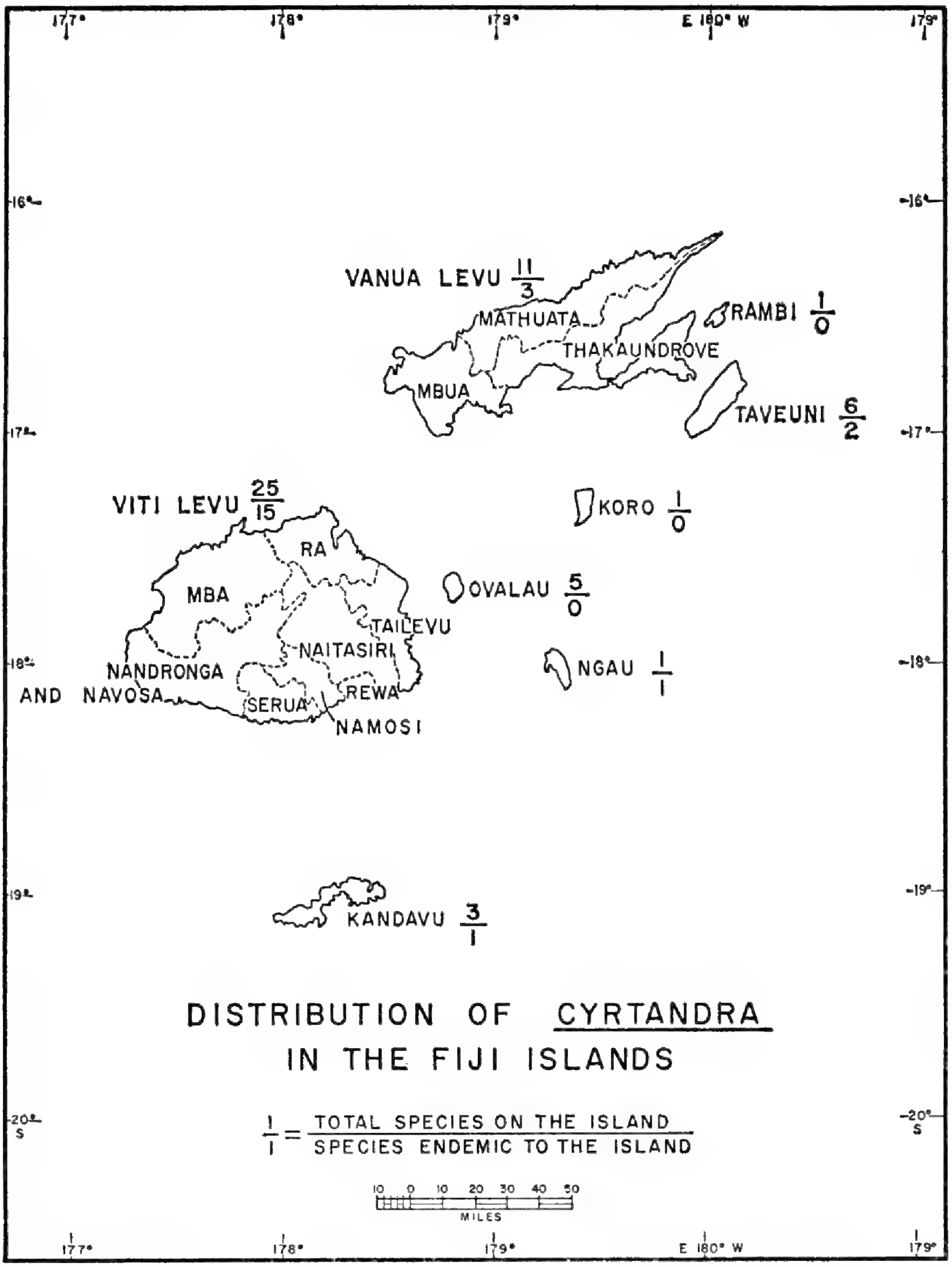
The herbarium material of several institutions has been examined in this study and is here cited, with the indicated abbreviations: Arnold Arboretum of Harvard University (A); Bernice P. Bishop Museum (BISH); British Museum (BM); Gray Herbarium of Harvard University (GH); Royal Botanic Gardens, Kew (K); New York Botanical Garden (NY); the University of California (UC); and U.S. National Herbarium (US). Appreciation is extended to the administrators of these herbaria for the privilege of examining specimens under their care. Special thanks are extended to Mr. B. L. Burtt, Royal Botanic Garden, Edinburg, who reviewed the manuscript and communicated many helpful suggestions. Appreciation is extended to Dr. Harold St. John, Bernice P. Bishop Museum, who reviewed the manuscript. The encouragement, valuable suggestions, and numerous reference materials made available to me by Dr. A. C. Smith, Wilder Professor of Botany, University of Hawaii, are gratefully acknowledged.

Systematic Treatment

Cyrtandra J. R. & G. Forst. Char. Gen 5. *pl. 3.* 1776. [2]

Herbs, vines, shrubs, or small trees, the stems round to sharply quadrangular, the trichomes septate, uniseriate, capitate or non-capitate hairs; leaves whorled, opposite or pseudoalternate by the reduction of one member of the pair, petiolate to sessile to connate-perfoliate, the blades simple; inflorescence a congested or elongate cyme, sessile or pedunculate, axillary on young branches or cauliflorous on older stems, sometimes arising among adventitious roots, usually bracteate, the outer bracts persistent or deciduous, foliaceous to corolloid and soft-textured, minute to as long as, or longer than,

[2] Greek *kyrtos*, curved, and *andros*, stamens.



the inflorescence, free or connate and cyathiferous, the inner bracts like the outer but smaller; flowers perfect, often protandrous, sometimes unisexual, the calyx foliaceous or corolloid, persistent or deciduous, spathaceous to variously cleft from summit nearly to base into 2 to 5 equal or unequal, valvate lobes; corolla fleshy to chartaceous, usually white, but also green, yellow, orange, red, pink, or lavender, 1-6 cm. long, cleft to half its length into rounded, equal to unequal, spreading to erect lobes, these imbricate in bud, the limb often bilabiate, the

TABLE 1.—*Distribution of* Cyrtandra *in Fiji, by islands*

Species	Viti Kandavu	Viti Levu	Viti Ovalau	Viti Ngau	Vanua Koro	Vanua Levu	Vanua Taveuni	Vanua Rambi
acutangula		×						
aloisiana		×						
anthropophagorum		×	×			×		
attenuata						×	×	
cephalophora		×				×		
chippendalei		×				×	×	
chlorantha		×						
ciliata					×	×	×	
coleoides		×						
cyathibracteata		×						
denhamii				×				
dolichocarpa						×		×
esothrix		×	×					
harveyi						×		
hornei		×						
involucrata		×	×			×		
jugalis		×						
kandavuensis	×							
leucantha		×					×	
milnei	×	×	×					
montana		×						
multiseptata		×						
muskarimba		×				×		
occulta		×						
prattii		×						
pritchardii		×	×					
reticulata						×		
spathacea	×	×						
taviunensis							×	
tempestii							×	
trichophylla		×						
ventricosa					×			
victoriae		×						
vitiensis		×						
xanthantha		×						

Total species: 35, all endemic to the Fiji Islands; 22 species are restricted to a single island; 8 species occur on 2 islands; 5 species occur on 3 islands.

lower or anterior lobe usually equal to or larger than the others; stamens 2, the filaments adnate to the tube opposite the sinuses of the anterior corolla lobe, the lower portion of each filament variously twisted, the anthers coherent at apices; staminodes 2 or 3, 0.5-5 mm. long, adnate to the corolla tube opposite the posterior sinuses, sometimes bearing small, vestigial anthers; base of the ovary clasped by a nectiferous, annular, cupulate, or one-sided disc, this often persistent in mature fruit, the ovary and style glabrous or variously pubescent, the stigma

capitate to applanate and bilobed, the plane of the expanded lobes perpendicular, oblique, or parallel to the axis of the style; fruit white, green, yellow, orange, red, or pink, a succulent to coriaceous berry, ovoid to oblong, up to 4 cm. long, or cylindrical and up to 12.5 cm. long, often beaked by the persistent style base; seeds many, usually less than 1 mm. long, usually embedded in the fleshy placentae.

Perhaps 600 species, distributed in rain forest habitats from the Nicobar Islands to the Malay Peninsula of the Asian mainland; through the Philippine Islands to Botel Tobago Island southeast of Formosa, and the Ryukyu Islands; throughout the Malay Archipelago, southeast to Queensland and the Loyalty Islands; east on the high islands of the Pacific to the Hawaiian Islands and the Marquesas Islands. The genus is not known on Formosa, Yap, the Marianas Islands, New Caledonia, or the Tuamotu Archipelago.

Key to Species Groups

Inflorescence capitate to subcapitate, the pedicels concealed by the congested flowers and bracts . . . . . GROUP 1
Inflorescence a branching cyme, not capitate or subcapitate; pedicels visible, not obscured by congested flowers and bracts.
  Calyx persistent, not abscissing from the maturing fruit . . . . . GROUP 2
  Calyx deciduous, abscissing at or shortly after anthesis.
    Flowers not borne on an elongate, woody, branchlike inflorescence axis.
      Styles and anthers restricted to the corolla tube, the filaments 1–4 mm. long, rarely 5 mm. long.
        Calyx lobes about as long as the calyx tube . . . . . GROUP 3
        Calyx lobes 2 to 5 times as long as the calyx tube . . . . . GROUP 4
      Styles, or anthers, exserted above the corolla tube, displayed in or above the broad corolla throat; filaments 8–12 mm. long; flowers sometimes unisexual . . . . . GROUP 5
    Flowers borne on a woody, branchlike inflorescence axis up to 20 cm. long, bearing numerous pedicels ca. 0.5 cm. long . . . . . GROUP 6

GROUP 1

Outer inflorescence bracts fused into a cup-shaped involucre.
  Leaf blades glabrous; calyx and bracts glabrous on the abaxial surfaces.
    1. C. cyathibracteata
  Leaf blades, calyx, and bracts sericeous on the abaxial surfaces . . **2. C. occulta**
Outer inflorescence bracts free; inflorescence without a cup-shaped involucre.
  Inflorescence cylindrical; peduncle 10–15 mm. long; calyx and bracts with indument of dark brown, rigid, glistening hairs . . . . **3. C. cephalophora**
  Inflorescence spreading, not cylindrical; peduncle 2–10 mm. long; calyx and bracts glabrous or with light brown, crumpled, capitate and noncapitate hairs.
Outer surfaces of calyx and bracts glabrous to gabrate; bracts lobed; petioles glabrate, winged to base . . . . . **4. C. vitiensis**
Outer surfaces of calyx and bracts moderately to densely pubescent with capitate and noncapitate hairs; bracts not lobed; petioles conspicuously pubescent, rarely winged.
  Hairs of the petiole shorter than the petiole diameter . . **5. C. leucantha**

Hairs of the petiole longer than the petiole diameter.
Inner surface of corolla glabrous; corolla green . . . **6. C. chlorantha**
Inner surface of corolla pubescent; corolla green to white . **7. C. milnei**

GROUP 2

Fruit long-attenuate, narrow-cylindrical, scarcely tapered to the style, up to 5.5 cm. long; corolla up to 5.5 cm. long . . . . . **8. C. dolichocarpa**
Fruit fusiform to ellipsoid to ovoid, conspicuously tapered to the base of the style, up to 2.5 cm. long; corolla up to 3.5 cm. long.
Calyx utriculose to ventricose, concealing the fruit, the lobes erect.
Leaf blades pubescent above, the under surface with tertiary veins concealed by pubescence; branches rounded, not sharply quadrangular.
Hairs of petioles about equal to petiole diameter; outer surface of corolla pubescent; fruit fusiform . . . . . **9. C. multiseptata**
Hairs of petioles 2–3 times as long as petiole diameter; outer surface of corolla glabrous; fruit ovoid . . . . . **10. C. ventricosa**
Leaf blades glabrous above, the under surface with conspicuous tertiary veins perpendicular to the secondary veins; branches sharply quadrangular. **11. C. acutangula**
Calyx campanulate to cylindrical with spreading lobes, the developing fruit exposed.
Inflorescence and leaves with appressed-sericeous pubescence.
Shrub or small tree up to 6 m. high with coarse, woody branches; peduncles up to ca. 0.5 cm. long . . . . . **12. C. trichophylla**
Shrub or herb 1–3 m. high with slender branches; peduncles 1–2 cm. long. **13. C. muskarimba**
Inflorescence and leaves with spreading, velutinous pubescence.
Calyx lobes thick, coriaceous; calyx 2.5 to 3.5 cm. long . **14. C. victoriae**
Calyx lobes foliaceous, not thick or coriaceous; calyx 1.5 to 2.5 cm. long. **15. C. chippendalei**

GROUP 3

Calyx spathaceous with a single cleft nearly to base . . . . . **16. C. spathacea**
Calyx not spathaceous, but variously cleft or lacerated.
Peduncle subtending a branching cyme bearing 6 to 10 flowers, or more.
Calyx lobes ovate; outer surface of calyx pubescent . . **17. C. kandavuensis**
Calyx lobes lanceolate-attenuate; outer surface of calyx glabrous. **18. C. attenuata**
Peduncle subtending 1 to 3, rarely 4, pedicellate flowers.
Pedicels subtended by a pair of connate-perfoliate bracts. **19. C. involucrata**
Pedicels subtended by free bracts.
Corolla with dense outer indument of capitate or noncapitate hairs.
Outer surface of corolla with indument of capitate hairs. **20. C. reticulata**
Outer surface of corolla with indument of noncapitate hairs.
Mature leaves glabrous above. . . . . **21. C. jugalis**
Mature leaves pubescent above. . . . . **22. C. anthropophagorum**
Corolla glabrous on outer surface.
Calyx lacerated into unequal segments, the outer surface glabrate, the inner surface pilose with ascending hairs; leaves pubescent below.
Calyx thick, fleshy, drying to a coriaceous texture, the apices of the lobes triangular . . . . . **23. C. esothrix**

Calyx thin, not fleshy and not coriaceous upon drying, the apices of the lobes lanceolate-attenuate. . . . . **24. C. hornei**

Calyx parted into 5 equal lobes, the leaves glabrous below.

Fruit orange to red; inflorescence filiform, with 2, 3, or more pairs of bracts; style glabrous.

Young stems drying to a flaky surface; bracts lanceolate. **25. C. taviunensis**

Young stems drying to a smooth surface; bracts linear. **26. C. montana**

Fruit white; inflorescence not filiform, with 1 pair of bracts; style with indument of capitate hairs . . . . . **27. C. pritchardii**

GROUP 4

Calyx lobes large, 1–1.5 cm. long.

Peduncles 4–9 cm. long; leaf blades lanceolate to ovate . . . **28. C. denhamii**

Peduncles 0.5–1.5 cm. long; leaf blades ovate to obovate. . . **29. C. tempestii**

Calyx lobes small, ca. 0.5 cm. long.

Outer surface of calyx glabrous, the lobes with rounded apices; peduncles up to 5 cm. long . . . . . **30. C. ciliata**

Outer surface of calyx with dense, velutinous pubescence, the lobes with acute apices; peduncles up to 1.5 cm. long.

Young petioles tomentose, the hairs about 0.5 as long as the petiole diameter. Montane habitats 500–1100 m. . . . . **31. C. xanthantha**

Young petioles densely villous, the hairs 1–4 times as long as the petiole diameter. Lowland habitats below 150 m. . . . . **32. C. aloisiana**

GROUP 5

Corolla with dense outer indument of capitate hairs; mature leaves pubescent beneath . . . . . **33. C. harveyi**

Corolla glabrous on outer surface; mature leaves glabrous beneath. **34. C. coleoides**

GROUP 6

A single species . . . . . **35. C. prattii**

1. Cyrtandra cyathibracteata Gillett, sp. nov.

Frutex ad 2 m. altus, partibus novellis indumento pruinoso indutis mox glabratis, ramulis ad 2 cm. diametro; folia opposita, petiolis alatis 1–4 cm. longis, laminis ovatis vel obovatis ad 40 cm. longis et 17 cm. latis, basi in petiolum alatum inequilateraliter attenuatis, apice acutis, margine hydathodis ca. 0.5 mm. longis et inter se ca. 1 mm. inconspicue serratis, maturitate utrinque glabris, venis primariis utrinsecus 7–12 adscendentibus, secundariis subtus inconspicuis; inflorescentiae capitatae, pedunculo crasso ca. 1 cm. longo apice bracteis caducis ornato, bracteis extimis in involucrum cyathiforme 1–2 cm. longum connatis ut bracteis interioribus ovatis extus glabris intus pilosis (pilis patentibus ca. 25μ diametro ad 2 mm. longis), pedicellis crassis 1–2 cm. longis; calyx carnosus ca. 12 mm. longus caducus in lobis haud 1 mm. longis fissus, sinibus sub anthesi irregulariter laceratis, tubo extus glabro intus piloso; corolla alba

carnosa ad 2 cm. longa in lobis subaequalibus rotundatis ca. 0.2 fissa extus indumento eglanduloso ornata intus glabra; staminia tubo corollae medium versus affixa, filamentis ca. 3 mm. longis, antheris in apice adhaerentibus ca. 2 mm. infra fauces corollae; staminodia 2, ca. 0.5 mm. longa infra filamenta 3 mm. et sinibus lateralibus oppositis disposita; discus annulari-cupuliformis prominens ca. 1.5 mm. altus deciduus; gynoecium ca. 12 mm. longum, ovario glabro, stylo indumento noncapitato ornato, stigmate bilobato pelviformi; fructus albi ovoidei ca. 8 mm. longi apice styli basi 1–2 mm. longo apiculati.

Type in the herbarium of the B. P. Bishop Museum, collected on bank of creek in Wainimala Valley, near Matawailevu, Waimano Creek, Province of Naitasiri, Viti Levu, Fiji, alt. about 500 m., Aug. 3, 1937, by *H. St. John* (18191). Duplicate at US.

DISTRIBUTION: Known only from the type specimen.

This species is closely related to *Cyrtandra occulta* and to *C. vitiensis*, differing from both in its glabrous foliage. It appears to be sympatric with the latter species. Further comments on the relationships in this group are included under *C. occulta*.

2. Cyrtandra occulta A. C. Smith, Journ. Arnold Arb. 34: 39. 1953.[3]

Erect shrub 2–3 m. high with densely sericeous pubescence of septate, uniseriate, noncapitate hairs ca. 20μ in diameter and up to 7 mm. long, the foliage and inflorescences subcoriaceous when dry; leaves opposite, the petioles 1–7 cm. long, winged, the blades ovate to oblanceolate, up to 40 cm. long and 18 cm. broad, tapering to the petiole acute to rounded at apex, undulate-crenate, glabrous above and densely sericeous beneath, the pubescence obscuring the secondary veins; inflorescences densely capitate, on stout axillary peduncles up to 3.5 cm. long, terminated by matted-sericeous, connate bracts forming a cuplike involucre up to 3 cm. long subtending a bracteolate, branched, many-flowered cyme 5–10 mm. long, the bracteoles greenish white, ovate-acuminate, up to 3 cm. long, with matted-sericeous pubescence on both surfaces; calyx greenish white, up to 2.5 cm. long, cleft 0.5 to 0.66 of its length into lanceolate-acuminate lobes with dense-sericeous pubescence on both surfaces; corolla white, cylindrical up to 2 cm. long, cleft ca. 0.25 of its length into unequal, rounded lobes with dense-sericeous outer pubescence and inner pubescence of very short, capitate hairs; filaments 3–4 mm. long, bearing apically coherent anthers 2–3 mm. below the corolla sinuses; staminodes 2,

[3] This and most of the other species of *Cyrtandra* are mentioned in J. W. Parham, Plants of the Fiji Islands (1964); most of the older species were mentioned in Horne, A Year in Fiji (1881), and by C. B. Clarke, in DC. Monogr. Phan., vol. 5 (1883).

adnate 8–10 mm. below the upper sinuses and near the middle of the corolla tube; cupulate annular disc conspicuous at anthesis, ca. 1 mm. high, deciduous from the maturing fruit; ovary and style ca. 12 mm. long, the style with indument of capitate hairs on the upper 0.66 of its length, separating 1–2 mm. above the apex of the mature ovary, the stigma applanate, bilobed, the lobes spreading from an oblique terminal cleft; fruit white, ovoid, ca. 1.6 cm. long and 1 cm. broad.

TYPE LOCALITY: Western slopes of Mount Tomanivi, Viti Levu, Fiji. Type collected by A. C. Smith, cited below.

DISTRIBUTION: Dense forests of Viti Levu, at altitudes of 250–1300 m.

VITI LEVU: Mba: Mount Tomanivi, *Smith* 5913 (A-type, BISH, US), *Parks* 20841 (BISH, UC, US). Namosi: Hills north of Wainavindrau Creek, *Smith* 8507 (BISH, US). Naitasiri: Rairaimatuku Plateau, *Smith* 5792 (A. US).

The present species and the related *Cyrtandra cyathibracteata* are distinguished from other members of this group by the cuplike involucre formed by the fusion of the two outer bracts of the inflorescence. This character has been observed in *C. godeffroyi* Reinecke (Samoa), *C. burbidgei* C. B. Clarke (Borneo), and *C. cumingii* C. B. Clarke (Philippine Islands). In *C. burbidgei*, the white involucre is certainly a most conspicuous feature, and it probably is of significance in attracting pollinators.

All of the species in Group 1 are characterized by bracts, calyces, and corollas that gradually rot and fall from the inflorescences, exposing the white fruits.

3. Cyrtandra cephalophora Gillespie, Bishop Mus. Bull. 74: 21, *fig. 26*. 1930.

Erect shrub 2–3 m. high, the young foliage glabrate, the stems up to 1.5 cm. in diameter, quadrangular, the pith up to 1 cm. in diameter; leaves opposite, the petioles 6–9 cm. long, the blades lanceolate to lanceolate-ovate to ovate, up to 24 cm. long and 12 cm. broad, equilateral and cuneate at base, acute to rounded at apex, entire to faintly serrate, at maturity glabrous above, glabrate beneath with scattered, noncapitate hairs ca. 25μ in diameter and 0.3 mm. long, the lower surface with 5–7 strongly ascending, raised primary veins on each side; inflorescences capitate-cylindrical, on stout peduncles 1–1.5 cm. long, the flowers partially concealed by conspicuous, persistent, ovate to orbicular subtending bracts 5–10 mm. long, the bracts with rigid, glistening, dark brown, noncapitate hairs ca. 30μ in diameter and 0.5–1 mm. long without, with similar but much larger hairs 1–3 mm. long within; calyx persistent, ca. 10 mm. long, cleft into equal, lanceolate-attenuate lobes ca. 4 mm. long, glabrate without with small, noncapitate hairs, pilose within with similar, ascending hairs to 3 mm. long; corolla white, 12 mm. long, cleft 0.33 of its length into rounded,

unequal lobes, glabrous on both surfaces; filaments 2–3 mm. long, bearing apically coherent anthers 1–2 mm. below the corolla limb; staminodes 2, clavate, ca. 1.5 mm. long, adnate ca. 1 mm. below the limb; cupulate annular disc prominent, ca. 1 mm. high, persistent; ovary and style ca. 8 mm. long, glabrous, the style curved toward the corolla throat and bearing an applanate, bilobed stigma, the lobes thick, ovate; fruit orange, ovoid, ca. 7 mm. long, terminated by the persistent style base.

TYPE LOCALITY: Namosi, Viti Levu, Fiji; type collected by Gillespie, cited below.

DISTRIBUTION: Namosi, Naitasiri, and Rewa, Viti Levu; Thakaundrove, Vanua Levu, in rain forest habitats between 150 and 1,200 meters.

VITI LEVU: Namosi: Naitarandamu Mountain, just below summit, *Gillespie* 3121 (BISH-type, NY, UC). Naitasiri: Tamavua Woods, 7½ miles from Suva, *Gillespie* 2416 (BISH). Rewa: Mount Kombalevu, *Parks* 20924, (BISH, UC). VANUA LEVU: Thakaundrove: Mount Mariko, *Smith* 463 (BISH).

The present species is one of the most easily recognized of Fijian Cyrtandrae by its conspicuously bracteate, capitate-cylindrical inflorescence and the peculiar indument of the inflorescence. The clavate, conspicuous staminodia borne near the summit of the corolla tube are not known to occur in other Fijian species.

4. Cyrtandra vitiensis Seem. (Bonplandia 9: 257. 1861, nom. nud.; Seem. ex A. Gray, Proc. Amer. Acad. 6: 41. 1862, nom. nud.) Fl. Vit. 182. 1866.
Cyrtandra amicta A.C. Smith, Journ. Arnold Arb. 34: 38. 1953.

Erect herbaceous to shrubby plants up to 4 m. high, with coarse branches up to 2 cm. in diameter and with extensive pith ca. 1.5 cm. in diameter, the young vegetative parts with sericeous pubescence of sepatate, uniseriate, noncapitate hairs ca. 20μ in diameter and up to 1.5 mm. long; leaves opposite, with winged petioles 4–15 cm. long, the blades lanceolate to oblanceolate to ovate, up to 70 cm. long and 22 cm. broad, with an inequilateral, decurrent base and an acute to obtuse to rounded apex, entire to undulate to faintly serrate at margin, glabrous above, faintly pubescent beneath with noncapitate hairs, the primary veins raised beneath, 6–20 per side, curved upward, the secondary veins forming a conspicuous reticulate pattern beneath; inflorescences congested-capitate, many-flowered, on stout peduncles 5–10 mm. long, these terminated by a pair of ovate, greenish white, lobed bracts up to 3 cm. long, these glabrous without and densely sericeous within, subtending a bracteolate, branching cyme, the bracteoles ovate-elliptic to lanceolate, 2- or 3-lobed, up to 3 cm. long, similar to the bracts in color and indument; calyx 1.5–4 cm. long, persistent, but rotting from the mature fruit, cleft ca. 0.25 of its length into unequal lanceolate to triangular lobes, these glabrous or

with scattered capitate hairs without and densely sericeous within at the base of the tube; corolla cylindrical, 1.7–4.5 cm. long, with 5 rounded, unequal lobes 2–10 mm. long, sericeous without when young, becoming glabrate at maturity, glabrous within; filaments 2–5 mm. long, arising opposite the lower sinuses and bearing apically coherent anthers at or below the corolla limb; staminodes 2, ca. 0.5 mm. long, adnate opposite the upper sinuses at about the same level as the stamens; cupulate annular disc prominent, ca. 1–1.5 mm. high at anthesis, deciduous from maturing fruits; ovary and style ca. 1–1.5 cm. long, the ovary glabrous, the style with sericeous indument on upper 0.33 of its length, but with capitate hairs below the stigma, the stigma with 2 flattened, applanate, ovate lobes perpendicular to the style, the style separating 1–2 mm. above the summit of the mature ovary; fruit white, ellipsoid, up to 2.5 cm. long.

TYPE LOCALITY: Namosi, Viti Levu, Fiji. Type collected by Seemann, cited below.

DISTRIBUTION: Upland rain forests of Viti Levu, between 125 and 1300 meters.

VITI LEVU: Mba: Mount Koroyanitu, Mount Evans Range, *Smith* 4244 (A, BISH, US); Mount Tomanivi, *Smith* 5914 (A-type of *Cyrtandra amicta*, BISH, US), *Smith* 5103 (A, US), *Gillespie* 4095 (BISH, NY, UC, US); Nandala Creek, near Nandarivatu, *Smith* 6223 (A, BISH, US), *Degener* 14925 (A, NY). Nandronga & Navosa: Rairaimatuku Plateau, *Smith* 5654 (A, BISH, US). Serua: Korovou, *St. John* 18941 (BISH, US). Namosi: Woods near Namosi, *Seemann* 277 (GH, K-type); Voma Mountain, *Gillespie* 2480 (BISH); without further locality, *Parks* 20239 (BISH, UC, US), *Parks* 20429 (UC), *Parks* 20271 (BISH, UC, US); Korombasambasanga Range, *Smith* 8649 (BISH, US). Naitasiri: Matawailevu, *St. John* 18184 (BISH, US). Rewa: Near Suva, *Tothill* 649 (BISH), *Setchell* & *Parks* 15156 (UC), *Setchell & Parks* 15135 (UC).

Useful distinguishing characters of *Cyrtandra vitiensis* include the large, lanceolate to oblanceolate, glabrate to faintly pubescent leaves with decurrent bases and reticulate venation beneath, and the congested, many-flowered, bracteate inflorescences, and glabrous outer surfaces of the bracts. The corolla has a sericeous outer pubescence when young but becomes glabrate to glabrous upon maturity, as in specimens originally referred to *C. amicta*. Both phases have calyces with pilose inner surfaces and are so closely similar in leaf and inflorescence characters that the possibility of their being conspecific had to be evaluated. After considerable study, I have concluded that their separation must rest on calyx and corolla measurements that contrast the larger flowers of *C. amicta* (calyx 3.5—4 cm. long; corolla 4—4.5 cm. long) with the smaller flowers of *C. vitiensis* (calyx 1.5—2.5 cm. long; corolla 1.7—2.8 cm. long). It is my conclusion that these differences in size, based on very limited material, probably reflect the normal variability within *C. vitiensis*.

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Specimens (*Smith* 4243, A, BISH, US) intermediate between *Cyrtandra vitiensis* and *C. milnei* have been collected on Mount Koroyanitu, Mount Evans Range, Mba, where both species occur. This collection surely portrays a combination of characters of the two species, including the decurrent petioles and the lanceolate to oblanceolate lamina of *C. vitiensis*, and the more dense indument of petioles and leaves, the shorter, triangular calyx-lobes, and the high frequency of capitate hairs, all of which characterize *C. milnei*. The collection is placed under *C. milnei* in the present study. There seems little doubt that the two species are very closely related.

The facies of certain species of the Hawaiian Islands suggests a close relationship with *Cyrtandra vitiensis* and other species of Group 1. These species include *C. oblanceolata* St. John & Storey and *C. waianuensis* Rock, which have the habit as well as the congested inflorescence and indument of *C. vitiensis*. In addition, the habit inflorescence, leaves, and flowers of *C. richii* A. Gray, of Samoa, suggest that it is of the same evolutionary stock as *C. vitiensis*.

5. Cyrtandra leucantha A. C. Smith, Journ. Arnold Arb. 34: 41. 1953.

Shrub up to 3 m. high with brown indument of septate, uniseriate capitate and noncapitate hairs up to ca. 100μ in diameter and 1–2 mm. long; leaves opposite, the petioles 3–10 cm. long, with pubescence shorter than petiole diameter, the blades oblanceolate to lanceolate-ovate to ovate, up to 32 cm. long and 15 cm. broad, inequilateral and cuneate to attenuate at base, acute to acuminate at apex, coarsely serrate to biserrate at margin, tomentose on both surfaces; inflorescenses many-flowered, congested, the peduncles ca. 2–5 mm. long, terminated by glabrate, ovate to elliptic to reniform, corolloid, persistent bracts up to 1 cm. long, these subtending branching, bracteolate cymes 5–10 mm. long, the bracteoles similar to and closely subtended by the outer bracts; calyx white, 1.5 cm. long, unequally cleft into 5 triangular-acuminate lobes 2–3 mm. long, persistent, with dense outer pubescence of capitate and noncapitate hairs, with inner pubescence of noncapitate hairs; corolla white, up to 2.5 cm. long, cleft into subequal, rounded lobes 2–3 mm. long, with dense, capitate and noncapitate hairs without, glabrous within; filaments ca. 3 mm. long, arising ca. 10 mm. below the sinuses of the lower corolla lobe and bearing apically coherent anthers well below the corolla throat; staminodes 2, ca. 1 mm. long, recurved, adnate opposite the upper sinuses at approximately the same level as the filaments; cupulate annular disc conspicuous, ca. 1 mm. high, deciduous from the mature fruit; ovary and style 12–15 mm. long, the ovary glabrous, the style with long, capitate hairs throughout its length, terminated by an applanate, bilobed stigma, the broadly ovate lobes of the stigma

perpendicular to the axis of the style, the style separating 1–2 mm. above the apex of the mature ovary; fruit white, ellipsoid, ca. 2 cm. long and 1.4 cm. wide.

TYPE LOCALITY: Mount Nanggaranambuluta, Mba, Viti Levu, Fiji. Type collected by A. C. Smith, cited below.

LOCAL NAME: "Mbeta kai" (*Smith* 4767).

DISTRIBUTION: Upland rain forests between 300 and 1,100 meters, in Mba, Viti Levu, and on Taveuni.

VITI LEVU: Mba: Mount Nanggaranambuluta, *Smith* 4767 (A. BISH, US), *Smith* 6312 (A-type, BISH, US), *Gillespie* 3689 (A, BISH, UC); Nandarivatu, *Tothill* 644 (BISH), *Degener & Ordonez* 13523 (A. BISH, NY, UC, US); Nandala, *Degener* 14836 (A, BISH, NY, UC, US). TAVEUNI: Hills east of Somosomo, *Smith* 8375 (BISH, US); Somosomo, edge of woods, *Gillespie* 4780 (BISH, US); valley between Mount Manuka and Mount Koroturanga, *Smith* 8253 (BISH, US).

The relationship between this species, *Cyrtandra chlorantha* A. C. Smith, and *C. milnei* A. Gray is very close. A tabular summary of distinguishing characters is presented under *C. chlorantha*. It has been pointed out in the discussion under *C. occulta* and *C. vitiensis* that this group of species is also represented in Polynesia, Borneo, and the Philippine Islands. An additional western relationship is portrayed by a collection from the Solomon Islands (*Brass* 3147, San Cristoval, BISH) in which the calyx, leaf, and inflorescence characters suggest the *C. leucantha* lineage.

6. Cyrtandra chlorantha A. C. Smith, Journ. Arnold Arb. 34: 42. 1953.

Shrub 3–4 m. high with pubescence of brown, septate, uniseriate capitate and noncapitate hairs up to 120μ in diameter and up to 4 mm. long; leaves opposite, the petioles 3–5 cm. long, the blades lanceolate to elliptic, up to 17 cm. long and 6 cm. broad, inequilateral and acute to cuneate at base, acute to acuminate at apex, coarsely serrate, tomentose to glabrate on both sides; inflorescences many-flowered, congested, the penduncles up to ca. 0.5 cm. long, terminated by persistent, green, ovate-elliptic bracts ca. 1.5 cm. long, these with a dense pubescence of long, capitate hairs without, glabrous to glabrate within, subtending short, branching bracteolate cymes, the bracteoles similar to the bracts but smaller; calyx green, broad-cylindrical, persistent, ca. 1.5 cm. long, cleft ca. 0.25 of its length into unequal triangular lobes, with dense, capitate hairs without, glabrous to glabrate with few capitate hairs within; corolla green, narrowly cylindric, ca. 1.5–2.2 cm. long, slightly exserted beyond the calyx, cleft ca. 0.2 of its length into rounded lobes, with capitate hairs without, glabrous within; filaments adnate near the middle of the corolla tube, ca. 3 mm. long, bearing apically coherent anthers 1–2 mm. below the corolla limb; staminodes 3, ca. 1 mm. long, adnate

opposite the upper sinuses at same level as filaments, the median staminode ca. 1 mm. above the laterals; cupulate annular disc prominent, ca. 1.5 mm. high; ovary and style ca. 1 cm. long, the ovary glabrous, the style with capitate hairs over its entire length, the stigma applanate, bilobed, the lobes perpendicular to the axis of the style, borne below the anthers.

TYPE LOCALITY: Naitasiri, Viti Levu, Fiji. Type collected by A. C. Smith, cited below.

DISTRIBUTION: Known only from the type locality, alt. 870–970 m.

VITI LEVU: Naitasiri: Northern portion of Rairaimatuku Plateau, between Mount Tomanivi and Nasonggo, in dense forest, *Smith* 5789 (A-type, BISH, US).

This species and the related *Crytandra milnei* and *C. leucantha* can be separated from each other by the following characters:

	C. chlorantha	*C. milnei*	*C. leucantha*
Color of calyx and corolla:	green	greenish-white to white	white
Inner corolla surface:	glabrous	pubescent	glabrous
Number of staminodes:	3	3	2
Length of petiole hairs:	3–4 mm.	3–6 mm.	1–2 mm.

7. Cyrtandra milnei (Seem. in Bonplandia 9: 257. 1861, nom. nud.) Seem. ex A. Gray, Proc. Amer. Acad. 6: 40. 1862.

Cyrtandra desvoeuxii Horne (A year in Fiji, 260. 1881, nom. nud.) ex C. B. Clarke in DC Monogr. Phan. 5: 265. 1883.

Cyrtandra glandulosa Gillespie, Bishop Mus. Bull. 74: 22, *fig. 28*, 1930.

Sparsely branched herb or shrub 1–4 m. high with indument of brown, septate, uniseriate trichomes, the capitate hairs 50–100μ in diameter and 1–2 mm. long, the noncapitate hairs up to 120μ in diameter and up to 6 mm. long; leaves opposite, the petioles up to 20 cm. long, densely villous, the hairs equal to or longer than the petiole diameter, the blades lanceolate to elliptic to ovate to obovate, up to 50 cm. long and 21 cm. broad, rounded, obtuse, acute, cuneate, or attenuate at base, obtuse, acute, or acuminate at apex, simply or doubly serrate, tomentose to glabrate above, moderately pilose beneath; inflorescences many-flowered, congested, the peduncles to 1 cm. long, terminated by corolloid, green to white, ovate to elliptic bracts up to 2 cm. long and 1 cm. wide, with a sparse to dense pubescence of capitate hairs without, glabrous within, subtending a bracteolate, branching cyme 0.5–3 cm. long, the bracteoles similar to but smaller than the bracts; calyx green to white, cylindrical, persistent, 1–2.5 cm. long, cleft ca. 0.25 of its length into 5 unequal lobes, the 3 smaller upper lobes triangular, the 2 larger lower lobes lanceolate-triangular, with capitate hairs on both surfaces; corolla green to white, 2–3 cm. long, cylindrical, cleft ca. 0.12 of its length into unequal,

rounded, erect lobes, with capitate and noncapitate hairs on both surfaces; filaments 3–4 mm. long, arising 8–10 cm. below the sinuses of the lower corolla lobe, bearing apically coherent anthers 1–2 mm. below the limb; staminodes 3, clavate, adnate opposite the upper sinuses at approximately the same level as the filaments, the medial staminode up to 2 mm. long, the lateral to 1 mm., borne slightly above the medial; cupulate annular disc prominent, ca. 1 mm. high, deciduous; ovary and style 1.2–2 cm. long, the ovary glabrous, the style with capitate hairs, separating 1–2 mm. above the apex of the mature ovary, the stigma applanate, bilobed, the lobes perpendicular to the axis of the style; fruit white, ovoid, up to 2 cm. long and 1.5 cm. wide.

TYPE LOCALITY: Ovalau, Fiji. Type collected by the U.S. Exploring Expedition, cited below.

LOCAL NAME: "Me-diri-ta-bua" (*Gillespie* 2601); "beta levu" (*Gillespie* 3852); and "kau-bi-bi" (*Gillespie* 2749).

DISTRIBUTION: Dense forests between 50 and 1,250 meters on Viti Levu, Kandavu, and Ovalau.

VITI LEVU: Mba: Mount Koroyanitu, Mount Evans Range, *Smith* 4129 (A, BISH, US), *Smith* 4243 (A, BISH, US); valley of the Singatoka River, near Nandarivatu, *Gillespie* 3852 (BISH-type of *Cyrtandra glandulosa* Gillespie, UC); Mount Tomanivi, *Gillespie* 4108 (BISH, UC, US), *Smith* 5101 (A, BISH, US), *Degener* 14335-a (A, NY); near Nandarivatu, *Gillespie* 4253 (BISH, UC, US); Nauwanga, near Nandarivatu, *Degener* 14686 (A, BISH, NY, UC, US); hills between Nggaliwana and Nandala creeks, south of Nauwanga, *Smith* 5848 (A, BISH, US). Namosi: Namosi Village, *Gillespie* 2601 (BISH); Voma Mountain, *Gillespie* 2749 (BISH); hills east of Wainikoroiluva River, near Namuamua, *Smith* 8940 (BISH, US), *Smith* 8963 (BISH, US). KANDAVU: Mount Mbuke Levu, *Smith* 287 (BISH, NY). OVALAU: Near summit of range west of Levuka *Gillespie* 4445 (BISH, NY, UC); Lovoni Valley, *Horne* 179 (GH, K-type of *Cyrtandra desvoeuxii* Horne ex C. B. Clarke); without further locality, *U.S. Expl. Exped.* s.n. (GH, US-type).

Seemann used Gray's description, verbatim, in Flora Vitiensis. Clarke wrote an abbreviated version of this, following it with a longer description of *Seemann* 281, which is *Cyrtandra chippendalei*, not *C. milnei*.

The designation of Ovalau as the type locality for this species rests on indirect evidence. The Wilkes Expedition is known to have collected six species of *Cyrtandra* in Fiji. The type material of *C. dolichocarpa* A. Gray and a sterile specimen of *C. harveyi* bear the locality of Sandalwood Bay, Vanua Levu. The remaining four species almost certainly were obtained on Ovalau, where the expedition spent a total of 42 days, nearly half of the visitation to Fiji. Pickering noted four collections of *Cyrtandra* on Ovalau. Ovalau is designated as the locality for three of these: *C. involucrata* Seem., *C. anthropophagorum* Seem.

ex A. Gray, and *C. pritchardii* Seem. The label of the fourth collection, the type of *C. milnei*, carries only "Feejee Islands" for locality; this is cited by Gray, but it may be assumed that the collection was obtained on Ovalau.

The bracts of the inflorescence are large and conspicuous, often exceeding the calyx. There is considerable range in flower size and this is sometimes expressed within a single inflorescence. The overall variability of this species is extensive and includes variation in leaf size, leaf shape, frequency and dimensions of capitate and noncapitate hairs. The colors of the bracts, calyces, and corollas have been variously reported as from greenish white to white. This variability extends to *Cyrtandra vitiensis* through one collection, *Smith* 4243, which is intermediate between *C. milnei* and *C. vtiensis*. The variability of present collections indicates that *C. milnei* is a complex assemblage of populations that make a difficult taxonomic problem. A portion of this complex was described by Gillespie as *C. glandulosa*. However, I have been unable to separate Gillespie's material from the rest of the complex.

8. Cyrtandra dolichocarpa A. Gray, Proc. Amer. Acad. 6: 40. 1862. *Cyrtandra microstigma* C. B. Clarke, in DC. Monogr. Phan. 5: 284. 1883.

Shrub or spreading tree 1–4 m. high with ferrugineous pubescence of septate, uniseriate, capitate and noncapitate hairs up to 100μ in diameter and 6 mm. long; leaves opposite, the petioles 1–4 cm. long, the blades lanceolate-ovate, up to 21 cm. long and 6 cm. broad, with inequilateral, obtuse, acute, or cuneate bases, acute to acuminate at apex, serrate, with 2 or 3 teeth per cm., moderately pubescent above, densely pubescent beneath, the veins obscure above, conspicuous beneath, the primary veins raised, curved upward, 6–8 per side, the secondary veins reticulate; inflorescences pilose, the peduncles 0.5–1 cm. long, terminated by persistent, ovate bracts 3–5 mm. long, subtending 1–5 bracteolate pedicels 2–2.5 cm. long, the bracteoles ca. 3 mm. long, pilose on both surfaces; calyx 2.5–3 cm. long, persistent, cylindrical, the lanceolate-acuminate lobes connivent, parted 10–15 mm. along 1 or 2 sinuses, with dense, noncapitate hairs on both surfaces; corolla chartaceous, distinctly bilabiate, white, up to 5.5 cm. long, cleft about 0.25 to 0.33 of its length into unequal, rounded lobes, the lower (anterior) lobe up to 2 cm. long and 1 cm. broad, the limb with conspicuous longitudinal veins, with numerous capitate hairs on both surfaces, the tube with capitate hairs without, glabrous within; filaments ca. 3 mm. long, arising 3–4 mm. below sinuses of the anterior corolla lobe, bearing apically coherent anthers at the throat; staminodes 3, 1.5 mm. long, arising ca. 5 mm. below sinuses of the upper lip, the median slightly shorter and borne 1–2

mm. above the lateral; cupulate annular disc conspicuous, ca. 1 mm. high; ovary and style ca. 2.5 cm. long, extending to ca. 5 mm. below corolla throat, densely pubescent with capitate and noncapitate hairs below, capitate hairs above, the ovary attenuate to the style and stigma, the stigma applanate, bilobed, the lobes thick, ca. 1 mm. long, spreading obliquely to the axis of the style; fruit cylindrical, elongate, up to 5.5 cm. long and 5–7 mm. broad.

TYPE LOCALITY: Mbua Bay (Sandalwood Bay), Vanua Levu. Type collected by the U.S. Exploring Expedition, cited below.

DISTRIBUTION: Dense forests of Vanua Levu and Rambi, 100–700 m.

LOCAL NAME: "Muskarimba" (*Smith* 612, 1594).

VANUA LEVU: Mbua: Mbua Bay, *U.S. Expl. Exped.* (GH, US-type); upper Ndama River Valley, *Smith* 1594 (BISH). Mathuata: Northwestern slope of Mount Numbuiloa, east of Lambasa, *Smith* 6530 (A, BISH, US). Thakaundrove: Southwestern slope of Mount Mbatini, *Smith* 612 (BISH, GH, NY, UC, US). Rambi: No locality, *Horne* 439 (K-syntype of *Cyrtandra microstigma* C. B. Clarke, the other syntype, *Horne* 439a, has not been seen.)

The present species has the largest flowers and surely the most peculiar, distinctive fruits of all the Fijian species. The extension of this lineage into Polynesia is indicated by similar flowers, inflorescences, and fruits in the Cyrtandrae of Samoa, such as *C. krugeri* Rein., *C. nudiflora* C. B. Clarke, and *C. pulchella* Rich., all of which have glabrous fruits, and *C. vaupelii* Lauterb., in which the fruits have a pubescence similar to that of *C. dolichocarpa*.

9. Cyrtandra multiseptata Gillespie, Bishop Mus. Bull. 74: 23, fig. 31. 1930.

Shrub or slender tree 2–4 m. high with brown indument of septate, uniseriate noncapitate hairs up to 60μ in diameter and 3 mm. long; leaves opposite, the petioles 1–6 cm. long, the blades lanceolate to ovate to obovate, up to 20 cm. long and 10 cm. wide, inequilateral, cuneate at base, acute to acuminate at apex, serrate, with 1–3 teeth per cm., at maturity glabrate above, tomentose beneath; inflorescences tomentose, the penduncles 2–5 mm. long, terminated by connate, deciduous bracts ca. 6 mm. long, subtending 1–3 bracteolate pedicels ca. 0.5 cm. long, the bracteoles connate, deciduous, equal to or smaller than the bracts; calyx 3.5 cm. long, ventricose, cleft ca. 0.33 of its length into unequal lanceolate-acuminate lobes, with noncapitate hairs ca. 40μ in diameter without, and a dense tomentum of smaller hairs ca. 15μ in diameter within; corolla with coarse, noncapitate hairs without, glabrous within; cupulate annular disc conspicuous, ca. 1 mm. high, persisting as a broken, irregular ring on mature fruits; fruit fusiform, sheathed by the calyx, up to 2.5 cm. long and 1 cm. wide.

TYPE LOCALITY: Wet canyons near Namosi Village, Viti Levu, Fiji. Type collected by Parks, cited below.

DISTRIBUTION: Dense forests between 800 and 1,000 meters, Mba and Namosi, Viti Levu.

VITI LEVU: Mba: Western slopes of Mount Nanggaranambuluta, east of Nandarivatu, *Smith* 6327 (A, BISH, US); Mount Tomanivi, *Smith* 5102 (A, US). NAMOSI: Canyons near Namosi Village, 800 m., *Parks* 20237 (BISH-type UC, US).

This species is distinguished from *Cyrtandra dolichocarpa* and *C. ventricosa* by the differences cited in the tabular summary given under the latter species. The habit, inflorescences, and chartaceous corollas of *C. multiseptata*, *C. ventricosa*, and *C. dolichocarpa* suggests that the three species are of a common evolutionary line. The extension of this lineage into Polynesia is discussed under *C. dolichocarpa*.

10. Cyrtandra ventricosa Gillett, sp. nov.

Herba suffruticosa 1-2 m. alta, pilis septatis 120μ diametro et ad 6 mm. longis induta; folia opposita, petiolis 1–7 cm. longis, laminis ovatis vel lanceolato-ovatis ad 22 cm. longis et 12 cm. latis, basi subaequilateraliter cuneatis, apice acutis vel acuminatis, margine hydathodis serratis, supra glabratis, subtus dense pubescentibus, venis primariis utrinsecus 6–10 curvatis; inflorescentiae pilosae pauciflorae, pedunculis axillaribus erectis 1–2 mm. longis, bracteis terminalibus lanceolatis caducis foliosis ca. 5 mm. longis, pedicellis bracteatis 10–12 mm. longis, bracteis interioribus caducis deltoideis basi connatis; calyx persistente cylindricus fauce constrictus 1.5 cm. longus in lobis 4 vel 5 valvatis lanceolatis 0.25 fissus utrinque pilosus; corolla chartacea viridi-alba vel eburnea 18 mm. longa, utrinque glabra, reticulato-venosa, in lobis 5 inaequalibus fissa, lobis 2 posterioribus 7 mm. longis et 6 mm. latis, lobis 3 anterioribus 10 mm. longis et 9 mm. latis; stamina 2 mm. infra sinus corollae lobi inferioris enata, antheris apice adhaerentibus in corollae faucium ore; staminodia 3 infra filamenta 2 mm. et sinibus superioribus opposita disposita, staminodio medio ca. 1 mm. longo et 1 mm. supra staminodia lateralia 2 mm. longa; discus annulari-cupuliformis prominens 1.5 mm. altus, sub fructu interruptus; gynoecium 1.5 cm. longum glabrum, styli parte superiore caduca, stigmate bilobato, lobis applanatis obliquis; fructus ovoidei 12 mm. longi, 7 mm. lati.

Type in the herbarium of the Bernice P. Bishop Museum, collected on the southern slope of the Valanga Range, Province of Thakaundrove, Vanua Levu, Fiji, alt. 100 m., Nov. 11, 1933, by A. C. Smith (368). Duplicates at A, NY, UC, US.

ADDITIONAL SPECIMENS EXAMINED:

VANUA LEVU: THAKAUNDROVE: Savu Savu Bay, Vatunivuamonde Mountain, *Degener & Ordonez* 13968 (A, BISH, UC, US).

LOCAL NAME: "Merikula" (*Smith* 368).

The affinities of this species are with *Cyrtandra multiseptata* and *C. dolichocarpa*. It is distinguished from the others by its indument, fruits, and habit, as shown in the following tabular summary:

	C. ventricosa	*C. multiseptata*	*C. dolichocarpa*
Dimensions of leaf trichomes:	120μ × 6–7 mm.	60μ × 3 mm.	100μ × 6 mm.
Fruit shape:	ovoid	fusiform	cylindrical
Habit:	subligneous herb 1–2 m. high	shrub or slender tree 2–4 m. high	shrub or tree 1–4 m. high

11. Cyrtandra acutangula Seem. (Bonplandia 9: 257. 1861, *nom. nud.;* Seem. ex A. Gray, Proc. Amer. Acad. 6: 41. 1862, *nom. subnud.*) Fl. Vit. 182. 1866. *Cyrtandra utriculosa* C. B. Clarke, in DC. Monogr. Phan. 5: 230. 1883.

Shrub 2–3 m. high with dark brown indument of septate, uniseriate, noncapitate hairs 15–25μ in diameter and up to 1 mm. long, the young branches sharply quadrangular, the bark with linear striations; leaves opposite, the petioles 1–6 cm. long, 3–4 mm. in diameter, the blades dark brown, lanceolate to elliptic to ovate, up to 23 cm. long and 8 cm. broad, equilateral and cuneate at base, acute to obtuse at apex, faintly serrate, when young glabrous above and densely brown-sericeous beneath, at maturity glabrous on both surfaces, the lower surface with conspicuous, raised veins, the secondary veins perpendicular to the primary veins; inflorescences tomentose, the peduncles 2–8 mm. long, reflexed, terminated by a pair of linear-lanceolate, free, caducous bracts up to 1.5 cm. long and subtending 1–3 bracteolate pedicels, the bracteoles lanceolate, free, caducous, up to 7 mm. long; calyx cylindrical, persistent, up to 3.5 cm. long, cleft to about half its length into lanceolate, acuminate lobes, the tube glabrous without, pilose with brown, ascending hairs 3–4 mm. long within; cupulate annular disc 2 mm. high, persistent, forming a continuous ring in mature fruit; fruit ovoid, about 1 cm. in diameter and 2 cm. long, tipped by the basal 3 mm. of the style and enclosed in the persistent calyx.

TYPE LOCALITY: Namosi, Viti Levu, Fiji. Type collected by Seemann, cited below.

DISTRIBUTION: Known with certainty only from the upland rain forests of Namosi Province, where it occurs at elevations near 1,000 m.

VITI. LEVU: Namosi: "Mountains near Namosi," *Seemann* 276 (GH, K-type); damp, shaded forests near Vienunga, *Horne* 911 (GH, K-type of *Cyrtandra utriculosa* C. B. Clarke); Mount Naitarandamu, *Gillespie* 3120 (BISH, UC). Viti Levu, without further locality: *Parks* 20478 (UC), 20954 (BISH, UC, US).

I have been unable to find a morphological basis for separating *Cyrtandra utriculosa* C. B. Clarke from *C. acutangula*. Both species are

based on material from a limited region of Namosi, so that the reduction of *C. utriculosa* seems justified. The facies of this species is very different from that of other species in Group 2, and I have seen no Polynesian material that bears a close resemblance to it.

The present species differs from the *Cyrtandra dolichocarpa-C. ventricosa-C. multiseptata* lineage in its much smaller trichomes, sharply quadrangular stems, dark brown foliage, and glabrous leaves. The trichomes of *C. multiseptata* are over twice the diameter of those of the present species, and those of *C. ventricosa* over five times.

12. Cyrtandra trichophylla A. C. Smith, Journ. Arnold Arb. 34: 44. 1953.

Shrub to slender tree 2–6 m. high with brown, appressed-sericeous pubescence of septate, uniseriate, noncapitate hairs 20–40μ in diameter and up to 2 mm. long; stems up to 8 cm. in diameter 1.5 m. above the ground, with much xylem and little pith; leaves opposite, the petioles 1–5 cm. long, the blades ovate to obovate to oblanceolate, up to 32 cm. long and 12 cm. broad, inequilateral and acute to cuneate at base, acute to obtuse to rounded at apex, dentate-crenate, glabrate to glabrous above, sericeous beneath, the primary veins conspicuously raised on lower surface, 9–12 per side, curved upward, the secondary veins sometimes obscured by pubescence; inflorescences with brown, dense, sericeous pubescence, few-flowered, nearly sessile, the stout peduncles terminated by connate, caducous bracts ca. 5 mm. long, subtending 1–3 pedicels 5–14 mm. long; calyx persistent, eventually rotting from mature fruit, 12–15 mm. long, cleft 0.5 to 0.66 of its length into lanceolate-acuminate lobes, densely sericeous on both surfaces; corolla ca. 2 cm. long, curved-cylindrical, cleft ca. 0.25 of its length into rounded, unequal lobes, densely sericeous without, the limb and throat with capitate hairs within; filaments ca. 3 mm. long, bearing apically coherent anthers at the base of the corolla limb; staminodes 3, ca. 0.5 mm. long, arising 5–6 mm. below the upper sinuses; cupulate annular disc thick, prominent, ca. 1 mm. high, breaking into plates persisting in mature fruit; ovary and style 12 mm. long, the ovary glabrous, the style with numerous capitate hairs in the upper half of its length, separating 1–2 mm. above the mature ovary, the stigma borne 1–2 mm. below the anthers, bilobed, applanate, the lobes oblique to the axis of the style; fruit white, ovoid-ellipsoid, up to 2 cm. long and 1 cm. wide.

TYPE LOCALITY: Ridge from Mount Namama toward Mount Tomanivi, Viti Levu, Fiji. Type collected by A. C. Smith, cited below.

DISTRIBUTION: Dense forests of Viti Levu from 100 to 1,300 m.

VITI LEVU: Mba: Nandala Creek, 3 mi. south of Nandarivatu, *Smith* 6246 (A, BISH, US). Namosi: Ridges near Namosi Village, *Gillespie* 2690 (BISH, NY, UC); Valley of the Waindina, near Namosi, *Gillespie* 2595 (BISH); Naitarandamu Mountain, *Gillespie* 3243 (BISH), *Gillespie* 3244 (BISH, UC), *Gillespie* 3378

(BISH, UC), *Gillespie* 3303 (BISH, UC); Wainavindrau Creek, near Wainimakutu, *Smith* 8544 (BISH, US); Vakarongasiu Mountain, *Gillespie* 3289 (BISH, UC); without further locality, *Parks* 20269 (BISH, UC). Ra: Ridge from Mount Namama toward Mount Tomanivi, *Smith* 5698 (A-type, BISH, US). Naitasiri: Wainisavulevu-Numbulolo Divide, *St. John* 18324 (BISH, US); near Tamavua, 150 m., *Gillespie* 2455 (A, BISH), Tamavua Village, *Gillespie* 2116 (BISH, UC). Rewa: Korombamba Mountain, *Gillespie* 2257 (BISH, UC), *Parks* 20138 (UC).

Among Fijian Cyrtandrae this species has the most conspicuously woody habit; the proportion of wood in the stem and branches is greater than it is known to be in any of the other species. It occurs in the territory of *Cyrtandra vitiensis* but is easily distinguished by its open, few-flowered inflorescences in contrast to the capitate, many-flowered inflorescences of *C. vitiensis*. The contrast in the proportion of wood in these species is shown below:

	C. vitiensis	*C. trichophylla*
Diameter of stem (mm.) / Diameter of pith cylinder (mm.)	20/15	10/4; 15/5; 16/4

Neither *Cyrtandra trichophylla* nor any closely related species are known to occur in Polynesia.

13. Cyrtandra muskarimba A.C. Smith, Bishop Mus. Bull. 141:132. *fig. 67.* 1936.

Shrub or succulent herb 1–3 m. high, the young parts with dark brown, appressed, septate, uniseriate, noncapitate hairs ca. 60–80μ in diameter and up to 3 mm. long; leaves opposite, the petioles 4–11 cm. long, the blades elliptic to ovate, up to 28 cm. long and 15 cm. broad, unequal and obtuse to cuneate at base, acute to acuminate at apex, finely serrate, above with appressed, usually parallel, sericeous hairs, beneath densely pubescent, with 9–11 upwardly curved, raised primary veins on each side of midvein, the secondary veins obscured by pubescence; inflorescences elongate, branching cymes with 1–4 flowers; peduncles 1–2 cm. long, terminated by lanceolate bracts ca. 1.5 cm. long, subtending pedicels ca. 1.5 cm. long; calyx persistent, ca. 1.5–1.8 cm. long, cleft 0.5 to 0.66 of its length into unequal, triangular to lanceolate lobes, with dark brown, appressed-ascending pubescence on both surfaces; corolla white, 2.0–2.3 cm. long, cleft into 5 rounded, unequal lobes 2–3 mm. long, cylindrical, coriaceous, externally glandular with capitate hairs or pilose with ascending, noncapitate hairs, within with capitate hairs; filaments 2–3 mm. long, bearing apically coherent anthers ca. 1 mm. below the corolla limb; staminodes 2, ca. 0.5 mm. long, arising near middle of corolla tube; cupulate annular disc conspicuous, ca. 1 mm. high, persisting as a broken ring in mature fruit; ovary and style 7–8 mm. long, the style with capitate hairs in upper 0.25 of its length; stigma borne 1–2 mm. below the anthers, weakly bilobed; fruit ovoid, ca. 1.5 cm. long

and 0.8 cm. wide, tipped by 1–2 mm. of the persistent style base, sheathed by the persistent calyx.

TYPE LOCALITY: In dense forest on the southwestern slope of Mount Mbatini, Vanua Levu, Fiji. Type collected by A.C. Smith, cited below.

LOCAL NAME: "Muskarimba" (*Smith* 1914).

DISTRIBUTION: Upland rain forests of Serua, Viti Levu, and Thakaundrove, Vanua Levu, between 300 and 700 meters.

VITI LEVU: Serua: Namboutini, *Damanu* 70 (K); Mbuyombuyo, near Namboutini, *Tabualewa* 15577 (A, BISH, NY, UC, US). VANUA LEVU: Thakaundrove: Southwestern slope of Mount Mbatini, *Smith* 673 (BISH-type, GH, NY, UC, US); Mount Ndikeva, *Smith* 1914 (BISH, GH, NY, UC, US).

This species is closely related to *Cyrtandra trichophylla*, differing from it in its decidedly less woody habit, larger trichomes, shorter peduncles, and the presence of only two staminodes.

14. Cyrtandra victoriae Gillespie, Bishop Mus. Bull. 74: 25, *fig. 34.* 1930.

Shrub to small tree 2–5 m. high with ferrugineous, septate, uniseriate, noncapitate hairs ca. 100–160μ in diameter and up to 5 mm. long; leaves opposite, the petioles 2–6 cm. long, with dense, velutinous pubescence, the blades ovate, obovate, oblanceolate, or lanceolate, up to 35 cm. long and 15 cm. broad, inequilateral and acute to cuneate at base, acute to acuminate at apex, serrate to entire, with moderate to dense tomentum above, the hairs lying parallel and upwardly directed on younger leaves, spreading on mature foliage, velutinous beneath; inflorescences with few flowers, the peduncles stout, 0.5–1 cm. long, terminated by velutinous, greenish white, ovate to lanceolate, attenuate, free to connate, caducous bracts 3–5 cm. long, these subtending 2–4 pedicels 5–10 mm. long; calyx white, growing with the developing fruit and persistent on mature fruits, 1.7–3 cm. long at anthesis, 3–4 cm. long in mature fruit, cleft 0.5 to 0.66 of its length into unequal, lanceolate-attenuate lobes, velutinous without, within glabrous above, below with a dense tomentum of ascending noncapitate hairs; corolla white, ca. 3.0–3.5 cm. long, cylindrical, slightly curved, cleft into rounded, unequal lobes 4–5 mm. long, with velutinous outer pubescence projecting well above the lobes, the inner surface with capitate hairs in upper third and mixed noncapitate and capitate hairs below; filaments 4–5 mm. long, bearing apically coherent anthers at the corolla throat; staminodes 3, adnate near the middle of the corolla tube, up to 1.5 mm. long, the median up to 0.5 mm. long, borne 2 mm. below the lateral; cupulate annular disc conspicuous, ca. 1 mm. high, persisting as a broken, thick, dark ring in mature fruit; ovary and style ca. 1.8 cm. long, the ovary glabrous, the style with dense indument of capitate hairs in upper 0.75 of its length,

separating 2–3 mm. above the apex of the fruit, the stigma weakly bilobed; fruit ovoid, up to 2 cm. long and 1.5 cm. wide.

TYPE LOCALITY: Mount Tomanivi, Mba, Viti Levu, Fiji. Type collected by Gillespie, cited below.

LOCAL NAME: "Doo'-re le'vu" (*Gillespie* 4088).

DISTRIBUTION: Dense upland forests of central Viti Levu, between 250 and 1,250 meters.

VITI LEVU: Mba: Mount Tomanivi, *Gillespie* 4088 (BISH-type, UC), *Smith* 5915 (A, BISH, US), 5916 (A, US), 5917 (A, BISH, US); summit of Mount Nanggaranambuluta, *Gillespie* 4349 (BISH); escarpment west of Nandarivatu, *Smith* 5081 (A, BISH, US). Namosi: Summit of Vakarongasiu Mountain, *Gillespie* 3263 (BISH); valley of Wainambua Creek, south of Mount Naitarandamu, *Smith* 8801 (BISH, US). Ra: Mount Namama, east of Nandarivatu, *Smith* 5697 (A, BISH, US), 5722 (A, BISH, US).

The significant features of *Cyrtandra victoriae* are the very large, fleshy (drying to coriaceous) calyx and corolla. The flowers and fruits of *Smith* 5081 and 5917 indicate that the calyx grows considerably after anthesis, a useful distinguishing character for the species.

	Length of Calyx	
	at anthesis	*in mature fruit*
	30 mm.	40 mm.
Smith 5081 (US)	20 mm.	30 mm.
	17 mm.	38 mm.
Smith 5917 (US)	30 mm.	37 mm.
	30 mm.	

The closest relationship of this species is with *Cyrtandra chippendalei*, and this is discussed under the latter species.

15. Cyrtandra chippendalei Horne ex C. B. Clarke, in DC. Monogr. Phan. 5: 230. 1883.

Cyrtandra tomentosa A. C. Smith, Sargentia 1: 116. 1942.

Herbaceous to shrubby plants 1–4 m. high with light brown, septate, uniseriate, noncapitate hairs 100–160μ in diameter and 2–5 mm. long; leaves opposite, the petioles 2–10 cm. long, with villous pubescence of hairs as long as the petiole diameter, the blades ovate to lanceolate to oblanceolate, up to 28 cm. long and 13 cm. wide, inequilateral and rounded to cuneate to attenuate at base, acute to acuminate at apex, finely serrate, moderately pubescent above and velutinous beneath; inflorescences with 1–6 flowers, densely villous; peduncles 1–3 cm. long, terminated by ovate, acuminate, basally connate, caducous bracts to 4 cm. long, these subtending bracteolate pedicels 0.5–2 cm. long; calyx 1.2–2.5 cm. long, distended by the maturing fruits, cleft ca. 0.5 to 0.66 of its length into 5 unequal, triangular to attenuate-

lanceolate, foliaceous lobes, densely pilose on both surfaces; corolla white, 2–3 cm. long, fleshy, drying to a coriaceous texture, cleft into unequal, rounded lobes 3–4 mm. long, pilose without, glabrous within or with capitate hairs; filaments 4–5 mm. long, bearing apically coherent anthers slightly below the corolla throat; staminodes 2, conspicuous, ca. 1.5 mm. long, adnate opposite the upper lateral sinuses at the same level as the filaments; cupulate annular disc conspicuous, ca. 1 mm. high, persisting as a fragmented brown disc in mature fruit; ovary and style 10–12 mm. long, the ovary glabrous, the style glabrous below, with dense indument of capitate hairs in the upper half of its length, separating 1–5 mm. above the summit of the mature ovary, the stigma applanate, bilobed, borne near the filament bases; fruit ovoid, ca. 2.2 cm. long and 1.8 cm. wide, the color not known.

TYPE LOCALITY: Mountain forests near Wai-Wai, Savu Savu Bay, Vanua Levu, Fiji. Type collected by Horne, cited below.

LOCAL NAME: "Mbeta" (*Degener* 14889); "Muskarimba" (*Smith* 1986).

DISTRIBUTION: Rain forests of Viti Levu, Vanua Levu, and Taveuni, between 150 and 1,250 meters.

VITI LEVU: Mba: Hills east of Nandala Creek, about 3 mi. south of Nandarivatu, *Smith* 6237 (A, US). Nandronga and Navosa: Nandrau, *Degener* 14889 (A-type of *Cyrtandra tomentosa* A. C. Smith, BISH, NY). Namosi: Naitarandamu Mountain, *Gillespie* 3351 (BISH, NY UC); Wainavindrau Creek, near Wainimakutu, *Smith* 8549 (BISH, US); Wainavindrau Creek, n. slope of Korombasambasanga Range, *Smith* 8720 (BISH, US). Rewa: Korombamba, *Parks* 20129 (UC). VANUA LEVU: Thakaundrove: Near Wai–Wai, Savu Savu Bay, *Horne* 577 (GH, K-type); Natewa Peninsula, Uluingala, *Smith 1986* (BISH, GH, NY, UC, US). TAVEUNI: Between Somosomo and Wairiki, *Smith* 885 (BISH, NY), hills east of Somosomo, *Smith* 8377 (BISH, US); without further locality, *Seemann* 281 (GH, K).

The type has triangular sepals and the inner surface of the corolla is glabrous. This is one of the most variable of Fijian Cyrtandrae. However, this variablity involves differences that do not seem to be in any case of sufficient magnitude to justify the recognition of more than one species. There is a close relationship between *Cyrtandra chippendalei* and *C. victoriae*. The foliaceous, smaller calyx (1.2-2.5 cm. long) of *C. chippendalei* does not have postanthesis growth and therefore is easily distinguished from the fleshy (drying to coriaceous) calyx of *C. victoriae*, which has considerable postanthesis growth.

There is as yet no evidence that the *Cyrtandra chippendalei* lineage extends into Tonga, Samoa, or eastern Polynesia. However, the Cyrtandrae of Hawaii that are classified under subgenus *Brachycyathus* C. B. Clarke (St. John, 1966) are of this lineage. The Hawaiian species possess the calyx, inflorescence, and indument characters of Group 2 of the Fijian Cyrtandrae and surely would be placed near C. *chip-*

pendalei. The discontinuous distribution of this group is comparable to that of certain other Pacific genera. These include *Cheirodendron* (Araliaceae), locally common in the Marquesas Islands and the Hawaiian Islands but not known elsewhere; *Pelea* (Rutaceae), restricted to Tahiti, the Marquesas, and Hawaii; *Gouania* (Rhamnaceae), in Fiji and Hawaii, but not known in Samoa or Tonga; and *Exocarpos* (Santalaceae) in Fiji, Rapa, and Hawaii, but not known elsewhere in Polynesia.

Hawaiian representatives of the *Cyrtandra chippendalei* line currently number 89 species on the island of Oahu (St. John, 1966).

16. Cyrtandra spathacea A. C. Smith, Bishop Mus. Bull. 141: 133. *fig. 69.* 1936.

Slender tree to 4 m. high, the young parts with indument of dark brown, septate, uniseriate hairs ca. 20μ in diameter and 0.2 mm. long; leaves opposite, the petioles 1.5–6 cm. long, the blades lanceolate-ovate, to ovate-elliptic, up to 22 cm. long and 14 cm. broad, unequal, obtuse to acute at base, acute to obtuse to rounded at apex, serrate, with 2 or 3 obtuse teeth per cm., each dentition with a distal hydathode, at maturity glabrous above, glabrate to glabrous below, the primary veins 6–10 per side, curved upward, the secondary veins conspicuous, reticulate; inflorescences branched cymes of 1–4 flowers, the peduncles 1–2 mm. long, terminated by a pair of caducous bracts ca. 1 mm. long, subtending a bracteolate cyme up to 4 cm. long; calyx spathaceous, ca. 1.5 cm. long, deciduous, cleft, and lacerated nearly to base at one sinus, on both surfaces with scattered, noncapitate hairs; corolla cream-white, glabrous on both surfaces, ca. 3 cm. long, cleft 0.5–1 cm. into unequal, rounded lobes, the broad throat tapering into a tube ca. 1 cm. long; filaments ca. 5 mm. long, adnate opposite the sinuses of the lower corolla lobe, bearing apically coherent anthers at the sinuses; staminodes 3, ca. 1 mm. long, arising ca. 5 mm. below upper sinuses, the median staminode 1–2 mm. below the lateral; cupulate annular disc prominent, ca. 1 mm. high, with inner pubescence of noncapitate hairs projecting above the rim, the disc drying to an inconspicuous, fragmented ring in mature fruit; ovary and style 1.5 cm. long, the ovary glabrous, the style with capitate and noncapitate hairs over its entire length, separating 1–2 mm. above apex of the mature ovary, the stigma applanate, bilobed, the lobes thick, symmetrical, perpendicular to the axis of the style, borne 4–5 mm. below the anthers; fruit white, ellipsoid, up to 12 mm. long and 8 mm. wide.

TYPE LOCALITY: Kandavu, Fiji; the type is *Smith* 258, cited below.

DISTRIBUTION: Upland rain forests of Viti Levu and Kandavu.

VITI LEVU: Mba: Mountains near Lautoka, *Greenwood* 51 (K). KANDAVU: Mount Mbuke Levu, *Smith* 258 (BISH-type, GH, NY, UC, US).

The spathaceous calyx is also present in *Cyrtandra longiflora* J. W. Moore of Polynesia, and specimens of the latter species collected in the Society Islands bear a striking similarity to the material from Viti Levu. The spathaceous calyx is present in several Hawaiian species of subgenus *Cyrtandra*. Additional evidence of the extension of this group into Polynesia is presented under *C. kandavuensis* and *C. attenuata*.

17. Cyrtandra kandavuensis A. C. Smith, Bishop Mus. Bull. 141: 132, *fig. 68.* 1936.

Shrub or small, spreading tree 2–4 m. high, the foliage and inflorescences with light brown septate, uniseriate, noncapitate hairs ca. 20μ in diameter and 1 mm. long; leaves opposite, the petioles 3–9 cm. long, the blades ovate to elliptic, up to 25 cm. long and 14 cm. wide, unequal, obtuse to oblique at base, acuminate at apex, serrate, with 1 or 2 teeth per cm., above with scattered, appressed hairs ca. 1 mm. long and parallel to primary veins, beneath densely pubescent on the veins, with nearly glabrate areoles, the primary veins 6–8 per side, curved upward, converging at margins; inflorescences many-flowered, branched, open cymes, with dense, erect, capitate and noncapitate hairs up to 0.33 mm. long, the peduncles 4–9 cm. long, terminated by a pair of deciduous, ovate, foliaceous bracts ca. 2–2.5 cm. long, the pedicels 2.5–4 cm. long; calyx deciduous, ca. 1.5 cm. long, cleft 0.66 of its length into 5 equal, ovate, acuminate, valvate lobes, with noncapitate and capitate hairs without, glabrous within; corolla white, ca. 1.5–2 cm. long, cleft ca. 0.25 of its length into rounded lobes, the throat funnelform, with capitate and noncapitate hairs without, glabrous within; filaments ca. 3 mm. long, arising 3 mm. below the sinuses of the lower corolla lobe and projecting upward scarcely more than 1 mm., bearing apically coherent anthers below the corolla limb; staminodes 3, ca. 1 mm. long, adnate ca. 5 mm. below the upper sinuses, the median staminode about 1 mm. above the lateral; cupulate annular disc conspicuous, ca. 1.5 mm. high, persisting as a divided pelviform structure in mature fruit; ovary and style glabrous, ca. 10 mm. long, the style separating ca. 3 mm. above the mature ovary, bearing an applanate, bilobed stigma ca. 2–3 mm. below the anthers; fruit white, ellipsoid, ca. 12 mm. long and 8 mm. wide.

TYPE LOCALITY: Mount Mbuke Levu, Kandavu, Fiji. Type collected by A. C. Smith, cited below.

DISTRIBUTION: Dense forests on Kandavu, 200–840 m.

KANDAVU: Mount Mbuke Levu, *Smith* 282 (BISH-type, GH, UC, US), *Smith* 288 (BISH, GH, NY, UC, US), Smith 214 (BISH, GH, NY, UC, US).

Related material in Polynesia includes an undetermined *Cyrtandra* from Tahiti, *St. John* 17154, and *C. pupukeaensis* St. John & Storey,

of Oahu, Hawaiian Islands. Both have the inflorescence, calyx, corolla, and indument of *C. kandavuensis*.

18. Cyrtandra attenuata Gillett, sp. nov.

Frutex 1–4 m. altus, pilis septatis ad 20μ diametro et 0.5 mm. longis indutus maturitate glaber; folia opposita, petiolis 1–3 cm. longis, laminis lanceolatis vel ovatis ad 15 cm. longis et 7 cm. latis, basi inaequilateraliter acutis vel cuneatis, apice acutis vel acuminatis, dentatis vel undulatis; inflorescentiae cymosae subpatentes 2–8 florae, pedunculis 1–6 cm. longis indumento adscendente obtectis, bracteis terminalibus binis linearibus 2–3 mm. longis caducis, pedicellis 1 vel 2 bracteolatis ad 6 cm. longis; calyx caducus albus vel viridi-albus membranaceus manifeste venosus ad 2 cm. longus basi inflatus in lobis deltoideis vel lanceolatis attenuatis aequalibus 0.33–0.5 fissus utrinque glaber vel glabratus; corolla alba chartacea ad 4 cm. longa in lobis paullo inaequalibus 0.25 fissa extus glabra intus capitato-glanduloso-pilosa; stamina ca. 5 mm. infra sinus corollae lobi inferioris enata, filamentis 4–5 cm. longis, antheris in corollae faucibus in apice adhaerentibus; staminodia 3 infra sinus superiores 4–5 mm. disposita 1.5–2 mm. longa, staminodio medio paullo supra staminodia lateralia; discus annularicupuliformis prominens sub anthesi ca. 1 mm. altus; gynoecium ca. 1.5 cm. longum, ovario glabro superne gradatim attenuato, stylo inferne glabro superne capitato-glanduloso-piloso, stigmate applanato bilobato 1–2 mm. infra antheras; fructus maturi desiderati.

Type in the herbarium of the Bernice P. Bishop Museum, collected near Uluingala, Natewa Peninsula, Province of Thakaundrove, Vanua Levu, Fiji, alt. 600–820 m., June 15, 1934, by A. C. Smith (2006). Duplicates at GH, NY, UC, US.

ADDITIONAL SPECIMENS EXAMINED:

TAVEUNI: Hills east of Somosomo, west of old crater occupied by small swamp and lake, dense forest, *Smith* 8366 (US).

The distinctive features of this species include the relatively large flowers with inflated calyces and the chartaceous corollas with glabrous outer surfaces. Material of the Samoan *Cyrtandra divertae* Christopherson bears a strong similarity to *C. attenuata*. A specimen with remarkably similar flowers and inflorescences was collected in Tahiti (*St. John & Fosberg* 14158 (BISH)). Finally, the new species is remarkably similar to *C. nukuhivensis* F. Brown, of the Marquesas Islands, the inflorescences and flowers being generally comparable in form and indument. These comparisons seem to indicate clearly that the lineage of the new species extends into western and eastern Polynesia.

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19. Cyrtandra involucrata Seem. (Bonplandia 9: 257. 1861, nom. nud.; Seem. ex A. Gray, Proc. Amer. Acad. 6: 41. 1862, nom. subnud.) Fl. Vit. 183. 1866.
Cyrtandra monticola Gillespie, Bishop Mus. Bull. 74: 23, *fig. 30*. 1930.
Cyrtandra gillespieana A. C. Smith, Bishop Mus. Bull. 141: 134. 1936.

Shrub or small tree up to 5 m. high, the leaves and inflorescences with medium to dark brown pubescence of shiny, septate, uniseriate, noncapitate hairs up to 50μ in diameter and 1 mm. long, densely tomentose on younger parts, glabrate at maturity; leaves opposite, the petioles up to 4.5 cm. long, the blades lanceolate to oblanceolate to elliptic, up to 20 cm. long and 10 cm. wide, unequal and rounded, obtuse, attenuate, or cuneate at base, acute to acuminate at apex, crenate to serrate, with about 3 teeth per cm., the teeth tipped by hydathodes, tomentose to glabrate with appressed hairs or glabrous above, with dense, spreading hairs beneath; inflorescences appressed-sericeous, the peduncles 3–40 mm. long, terminated by 2 ovate, connate-perfoliate, foliaceous, deciduous bracts 5–8 mm. long, subtending 1–4 pedicels up to 2 cm. long; calyx deciduous, 6–8 mm. long, cleft about half of its length into 5 unequal, lanceolate, acuminate lobes, with noncapitate hairs on both sides; corolla cream to light yellow, ca. 1.5 cm. long, cleft ca. 0.25 of its length into rounded, subequal lobes, the tube cylindrical, with dense noncapitate and capitate hairs without, with short, capitate hairs within; filaments 2–3 mm. long, bearing apically coherent anthers 1–2 mm. below the corolla limb; staminodes 3, adnate opposite the upper sinuses ca. 3 mm. below the limb, the median staminode 1–2 mm. above the lateral; annular disc ca. 1 mm. high, persisting as rectangular plates in mature fruit; ovary and style up to 1 cm. long, the ovary glabrous, the style with capitate hairs over its entire length, separating at summit of ovary, the stigma applanate, bilobed, borne 2–3 mm. below anthers; fruit white, ovoid to ellipsoid, ca. 1.8 cm. long and 1.2 cm. wide.

TYPE LOCALITY: "Woods of Namosi," Viti Levu, Fiji. Type collected by Seemann, cited below.

LOCAL NAME: "Tangitangi" (*Tabualewa* 15596).

DISTRIBUTION: Interior mountains of Viti Levu, Ovalau, and Vanua Levu, between 30 and 1,150 m. in densely shaded creeks and drainages as an understory element in the rain forest.

VITI LEVU: Mba: Mount Evans Range, *Greenwood* 1228 (A, BISH, NY, UC, US); Mount Evans Range, eastern slopes of Mount Koroyanitu, *Smith* 4136 (A, BISH, US); Thol-i-nandarivatu Mountain, *Gillespie* 3866 (BISH, UC); hills east of Nandala Creek, ca. 3 mi. south of Nandarivatu, *Smith* 6221 (A, BISH, US); western and southern slopes of Mount Tomanivi, *Smith* 5318 (A, BISH, US). Nandronga & Navosa: Nausori highlands, in drainage of Namosi Creek above Tumbenasolo, *Smith* 4717 (A, BISH, US). Serua: Mbuyombuyo, near Namboutini, *Tabualewa* 15596 (A, BISH, UC, US); hills north of Ngaloa, in drainage of Waininggere Creek, *Smith* 9426 (BISH, US). Namosi: Without locality, *Seemann* 279 (GH, K-type); vicinity of Namosi Village, *Gillespie* 2691

(BISH); Naitarandamu Mountain, *Gillespie* 3122 (BISH-type of *Cyrtandra monticola* Gillespie, UC). Ovalau: Without further locality, *U.S. Expl. Exped.* s.n. (GH, US). Vanua Levu: Mbua: H. B. R. *Parham* 17 (A).

The connate, foliaceous bracts subtending the pedicels provide a distinguishing feature for this species. However, the bracts are deciduous and if they are lacking, the species is easily confused with *Cyrtandra anthropophagorum*, in which the inflorescence bracts are also deciduous but are free and not connate. In such cases the following characters are of value:

	C. involucrata	*C. anthropophagorum*
Color of pubescence	dark brown	golden brown
Peduncle length	up to 4.5 cm.	up to 3 cm.
Trichomes of peduncle	up to 1 mm. long, appressed	up to 1.5 mm. long, spreading

These two species are relatively common in Fiji, but neither they nor related species are known to occur in Polynesia.

20. Cyrtandra reticulata Gillett, sp. nov.

Frutex 2–3 m. altus, partibus novellis pilis fuscis septatis ecapitatis ca. 30μ diametro ad 0.5 mm. longis dense sericeus, maturitate glaber; folia opposita, petiolis ad 4.5 cm. longis, laminis lanceolatis vel ellipticis ad 20 cm. longis et 7 cm. latis, basi inaequilateraliter rotundatis vel obtusis vel cuneatis, apice acutis vel attenuatis, integris vel dentibus 1 vel 2 per cm. crenatis vel serratis, supra puberulis vel glabris, subtus in nervis dense pubescentibus alibi subglabratis, venis primariis utrinsecus 6–8 curvatis, rete venularum conspicuo; inflorescentiae pilis patentibus dense pubescentes, pendunculis 6–12 mm. longis, bracteis terminalibus lanceolatis 4 mm. longis caducis, pedicellis 2 vel 3 et 5–12 mm. longis; calyx caducus ca. 8 mm. longus in lobis 5 aequalibus ovato-lanceolatis acuminatis 0.5 fissus extus ecapitato-pilosus intus glaber; corolla pallide lutea infundibuliformis ca. 1.8 cm. longa in lobis inaequalibus rotundatis ca. 0.25 fissa, extus capitato-glanduloso-pilosa, intus tubo glabra limbo capitato-glanduloso-pilosa; filamenta ca. 3 mm. longa, antheris in apice adhaerentibus ca. 1 mm. infra sinus corollae; staminodia 3, ca. 0.75 mm. longa prope filamenta enata, staminodio medio ca. 1 mm. supra staminodia lateralia; discus annulari-cupuliformis conspicuus ca. 1 mm. altus sub fructu fragmentibus persistens; gynoecium ca. 12 mm. longum, ovario glabro, stylo albo ubique capitato-piloso demum 1–2 mm. supra basim caduco, stigmate applanato bilobato ca. 3 mm. infra antheras; fructu albo ca. 1 cm. longi et 0.6 cm. lati.

Type in the herbarium of the Arnold Arboretum, collected on the southern slopes of Mount Numbuiloa, east of Lambasa, Province of Mathuata, Vanua Levu, Fiji, alt. 100–350 m., Oct. 27, 1947, by A. C. Smith (6343). Duplicates at BISH, US.

ADDITIONAL SPECIMENS EXAMINED:

VANUA LEVU: Mathuata: Same locality as type, *Smith* 6529 (A, BISH, US). Thakaundrove: Eastern drainage of Yanawai River, *Degener & Ordonez* 14088 (A, BISH, NY, UC, US).

The new species bears a superficial resemblance to *Cyrtandra harveyi* but lacks the exserted stamens and style, the long filaments, the pedestal or "gynophore" at the base of the ovary, and the much larger flowers of that species. Inflorescence and floral characters seem to place it near *C. involucrata* and *C. attenuata*. I have not seen other Melanesian or Polynesian Cyrtandrae that resemble the new species.

21. Cyrtandra jugalis A. C. Smith, Journ. Arnold Arb. 34: 49. 1953.

Shrub or slender tree 2–5 m. high, densely pubescent on younger parts with septate, uniseriate, light to dark brown, noncapitate hairs ca. 30μ in diameter and 0.5 mm. long; leaves opposite, the petioles 1–2 cm. long, the blades lanceolate to oblanceolate to ovate, up to 16 cm. long and 5 cm. wide, unequal and acute to cuneate at base, acute to acuminate at apex, undulate to serrate, with 2–3 teeth per cm. at margin, glabrous above, with dense tomentum of noncapitate hairs beneath, these more pronounced on the veins, the primary veins raised, 5–7 on each side of midvein, the secondary veins inconspicuously reticulate; inflorescence a simple dichasium, tomentose to glabrate, the peduncles 1–5 cm. long, terminated by a pair of deciduous lanceolate, free bracts ca. 0.5 cm. long, subtending pedicels 1–2.5 cm. long; calyx fleshy, drying subcoriaceous, ca. 1 cm. long, cleft ca. 0.33 of its length into 5 equal, triangular-attenuate lobes, glabrate on both surfaces; corolla white, ca. 2 cm. long, cleft ca. 0.33 of its length into unequal, rounded lobes, with dense, ascending, noncapitate hairs without, with capitate hairs within; filaments ca. 2 mm. long, adnate to corolla tube opposite lower sinuses, bearing apically coherent anthers at the base of the corolla limb; staminodes 3, adnate opposite upper sinuses at same level as filaments, the median staminode 1 mm. long, slender, the lateral 2 mm. long, clavate; cupulate annular disc prominent, 1 mm. high, persisting as rectangular fragments in mature fruit; ovary and style up to 10 mm. long, the ovary glabrous, the style with capitate hairs, separating ca. 1 mm. above apex of mature fruit, the stigma applanate, bilobed; fruit white, ellipsoid, ca. 1.2 cm. long and 0.8 cm. wide.

TYPE LOCALITY: Ridge between Mount Nanggaranambuluta and Mount Namama, east of Nandarivatu, Viti Levu. Type collected by A. C. Smith, cited below.

LOCAL NAME: "Mindra" (*Smith* 4994); "Mbetambeta" (*Degener* 14904).

DISTRIBUTION: Dense forests in the highlands of central Viti Levu, in the vicinity of Mount Tomanivi and the mountains west of Nandarivatu, between 700 and 1,150 meters.

VITI LEVU: Mba: Nambuisa Village, *Gillespie* 4134 (BISH, UC); ridge between Mount Nanggaranambuluta and Mount Namama, east of Nandarivatu, *Smith* 4994 (A-type, BISH, US); summit of Mount Nanggaranambuluta, *Smith* 4878 (A, BISH, US); western and southern slopes of Mount Tomanivi, *Smith* 5319 (A, BISH, US). Nandronga & Navosa: Vicinity of Nandrau, *Degener*, 14904 (A); northern portion of Rairaimatuku Plateau, between Nandrau and Nanga, *Smith* 5569 (A, BISH, US). Ra: Ridge from Mount Namama toward Mount Tomanivi, *Smith* 5695 (A, BISH, US), *Smith* 5696 (A, BISH, US), *Smith* 5709 (A, BISH, US), *Smith* 5715 (A, BISH, US).

The present species appears to be closely related to *Cyrtandra involucrata* and *C. anthropophagorum;* it lacks the connate-perfoliate bracts of the former and the larger corollas (up to 20 mm. long) and indument of the latter. However, neither of the related species have the simple dichasium inflorescence that so well characterizes *Cyrtandra jugalis*. None of the Polynesian species have a close resemblance to this species.

22. Cyrtandra anthropophagorum Seem. (Bonplandia 9: 257. 1861, nom. nud.) ex A. Gray, Proc. Amer. Acad. 6: 41. 1862. Fl. Vit. 182. 1866.
Cyrtandra buttii Horne ex C. B. Clarke, in DC. Monogr. Phan. 5: 279. 1883.

Shrub or small tree to 4 m. high, the stem up to 6 cm. diameter 1.5 m. above the ground, freely branched, the young parts covered with golden-brown, velutinous, septate, uniseriate, noncapitate hairs 20–60μ in diameter and up to 1.5 mm. long; leaves opposite, the petioles 1–5 cm. long, the blades ovate-lanceolate, at maturity up to 30 cm. long and 12 cm. wide, unequal and acute, attenuate, or cuneate at base, acute to acuminate at apex, crenate to serrate, with about 3 teeth per cm., tomentose above, with appressed-ascending hairs parallel to the primary veins, densely tomentose beneath with spreading hairs, the primary veins 8–12 on each side of midvein, upwardly curved, the secondary veins concealed by pubescence; inflorescence densely tomentose, the peduncles 1–30 mm. long, terminated by a pair of lanceolate, free, deciduous bracts ca. 1.5 cm. long, subtending 1–4 pedicels 1–3 cm. long; calyx green to dull white, 5–7 mm. long, cleft half its length into 5 unequal, lanceolate, acute to acuminate lobes, both surfaces tomentose; corolla white, 12–15 mm. long, the tube cylindric, the lobes 4–5 mm. long, unequal, rounded, tomentose with noncapitate hairs without, and short, capitate hairs within; filaments ca. 2 mm. long, bearing apically coherent anthers slightly below the

corolla limb; staminodes 3, adnate opposite the upper sinuses near the middle of corolla tube, the lateral staminodes nearly 1 mm. long, the median ca. 0.25 mm. long; cupulate annular disc conspicuous, ca. 1 mm. high, drying to deciduous, rectangular segments; ovary and style ca. 8 mm. long, the ovary glabrous, the style with capitate hairs on the upper 0.75 of its length, separating ca. 1 mm. above summit of mature ovary, the stigma applanate, bilobed, borne below the anthers; fruit white, ovoid, up to 1.5 cm. long and 1 cm. wide.

TYPE LOCALITY: Viti Levu, Fiji. Type collected by Seemann (278).

LOCAL NAME: "Makamakandora" (*St. John* 18926).

DISTRIBUTION: Understory of rain forests in coastal and interior regions of southeastern Viti Levu and Ovalau, between 30 and 1,100 meters.

VITI LEVU: Without locality, *Seemann* 278 (GH-lectotype, K). Serua: Hills north of Ngaloa, in drainage of Waininggere Creek, *Smith* 9164 (BISH, US); track north of Korovou, *St. John* 18926 (BISH); Nakavu, *Parks* 20364, 20365 (BISH, UC, US). Namosi: Naitarandamu Mountain, *Gillespie* 3366 (BISH, UC), 3084 (A, BISH, NY, UC, US), 3139 (BISH), 3135 (BISH); without locality, *Horne* 818 (GH, K-type of *Cyrtandra buttii* Horne ex C. B. Clarke), *Horne* 956 (GH, K-syntype of *Cyrtandra buttii* Horne ex C. B. Clarke); without locality, *Gillespie* 2490 (BISH, UC), 2998 (BISH, UC, US), 2848 (BISH), *Parks* 20262 (BISH, UC), 20262-a, 20268, 20276 (BISH, UC, US); hills north of Wainavindrau Creek, between Korombasambasanga Range and Mount Naitarandamu, *Smith* 8411 (BISH, US); hills bordering Wainavindrau Creek, in vicinity of Wainimakutu, *Smith* 8565 (BISH, US); northern slopes of Korombasambasanga Range in drainage of Wainavindrau Creek, *Smith* 8719 (BISH, US); Namuamua, *Gillespie* 2992 (A, BISH); hills east of Wainikoroiluva River, near Namuamua, *Smith* 8909 (BISH, US); Navua River, *Greenwood* 1049 (A). Naitasiri: Nasinu, 9 mi. from Suva, *Gillespie* 3509 (BISH, UC); Tamavua-Sawani Road, *Setchell & Parks* 15143 (UC); Nasinu road, 2 mi. from Suva, *Gillespie* 3450 (BISH, NY, UC, US). Tailevu: Hills east of Wainimbuka River, in vicinity of Ndakuivuna, *Smith* 7062, 7110 (BISH, US). Rewa: Suva, *Meebold* 16725 (BISH), *Tothill* 640 (A, BISH), 641, 507 (BISH), *MacDaniels* 1138 (BISH). OVALAU: Summit of Mount Ndelaiovalau, *Smith* 7380 (BISH, US); without locality, undershrub in rain forest, *E. H. Bryan* 599 (BISH) without locality, *U.S. Expl. Exped.*, June 1840 (GH, US). VANUA LEVU: Mathuata: Wainikoro, Greenwood 687 (K).

Gray described the flower from the material of the U.S. Exploring Expedition, the young fruit from *Seemann* 278. The latter is here designated as the lectotype. This is one of the most frequently collected Cyrtandrae in Fiji. Its relationship is with *C. involucrata* and is discussed under that species.

23. Cyrtandra esothrix A.C. Smith, Journ. Arnold Arb. 34:45. 1953.

Shrub or small tree up to 6 m. high, the leaves and inflorescence with light tomentum of septate, uniseriate, erect, noncapitate hairs ca. 40 μ in diameter and 0.5 mm. long, the young stems quadrangular; leaves

opposite, the petioles 0.5 to 2.5 cm. long, the blades lanceolate to ovate, up to 22 cm. long and 8 cm. wide, unequal and obtuse to acute or cuneate at base, acute to acuminate at apex, entire to undulate to serrate, glabrous above, beneath with glabrous to glabrate areoles, the veins tomentose to glabrous, the primary veins raised, 6–9 per side, the secondary veins indistinct to conspicuous; inflorescences axillary, the peduncle up to 1 cm. long, terminated by minute, caducous bracts subtending 1–4 pedicels up to 1 cm. long; calyx greenish white, coriaceous, deciduous, up to 1 cm. long, cleft ca 0.25 of its length into equal, connivent, lobes, with 1 or 2 sinuses lacerated to base, glabrous without, pilose within, with ascending light brown hairs; corolla white, cylindrical, ca. 2 cm. long, cleft 0.20 of its length into unequal, rounded, spreading lobes pubescent without, with capitate and non-capitate hairs, glabrous within; filaments ca. 2 mm. long, adnate opposite the sinuses of the anterior corolla lobe and bearing apically coherent anthers at base of corolla limb; staminodes 3, ca. 0.5 mm. long, adnate opposite the upper sinuses near middle of corolla tube, the median staminode ca. 2 mm. below the lateral; cupulate annular disc conspicuous, ca. 0.75 mm. high, deciduous; ovary and style ca. 1 cm. long, the ovary glabrous, the style with capitate hairs, deciduous ca. 2 mm. above apex of the mature ovary, the stigma applanate, bilobed, borne ca. 5 mm. below the anthers; fruit white, elliposidal, up to 1.5 cm. long and 1 cm. broad.

TYPE LOCALITY: Northern portion of Rairaimatuku Plateau, Viti Levu, Fiji. Type collected by A. C. Smith, cited below.

DISTRIBUTION: Interior mountains of eastern Viti Levu and Ovalau, in dense forest, 100 to 1,100 m.

LOCAL NAME: "Makamakandora" (*St. John* 18185).

VITI LEVU: Mba: Mount Tomanivi, *Gillespie* 4081 (BISH, GH, NY, UC), *Smith* 5098 (A, BISH, US), *Smith* 5267 (A, BISH, US). Namosi: Naitarandamu Mountain, *Gillespie* 3113 (BISH, UC, US). Naitasiri: Rairaimatuku Plateau, between Mount Tomanivi and Nasonggo, *Smith* 6134 (A-type, BISH, US); Wainamo Creek, near Matawailevu, *St. John* 18185 (BISH, US). Tailevu: Hills east of Wainimbuka River, near Ndakuivuna, *Smih* 7067 (BISH, US), *Smith*, 7134 (BISH, US), *Smith* 7179 (BISH, US). OVALAU: Mountains south of Levuka, on overland trail to the west coast, *Gillespie* 4538 (BISH, UC); hills east of Lovoni Valley, *Smith* 7261 (BISH, US), *Smith* 7679 (BISH, US).

The significant distinguishing features of this species include the thick, coriaceous calyx, which is lacerated below the short lobes, and the pilose interior of the calyx. There is some variability in the indument of the secondary veins of the lower leaf surface. In all collections from Ovalau and the adjacent territory of Tailevu, Viti Levu, these veins are glabrous; however, they are tomentose in the collections from central Viti Levu.

There appears to be a close morphological relationship between *Cyrtandra esothrix* and *C. hornei;* the two species can be distinguished by the differences cited in the following tabulation:

	C. hornei	*C. esothrix*
Surface of outer/calyx:	puberulent	glabrous
Surface of inner/corolla:	glandular	glabrous
Apices of calyx lobes:	attenuate	acute
Staminodes:	1.5 mm. long	0.5 mm. long

In the examination of the Polynesian representatives of the genus, I have seen no material that would appear to be closely related to these two species. The bark of *Cyrtandra esothrix* has been used medicinally to cause constipation after sickness, according to St. John.

24. Cyrtandra hornei C. B. Clarke, in DC Monogr. Phan. 5: 281. 1883.
Cyrtandra greenwoodiana A. C. Smith, Journ. Arnold Arb. 34: 46. 1953.

Shrub or small tree up to 6 m. high, with rubiginose tomentum of septate, uniseriate, noncapitate hairs ca. 15μ in diameter and 0.1–0.3 mm. long, becoming glabrate to glabrous; leaves opposite, the petioles 0.5–3 cm. long, the blades elliptic to ovate, up to 15 cm. long and 6 cm. wide, inequilateral and obtuse to acute or cuneate at base, obtuse to acute or acuminate at apex, entire to undulate, dentate, or serrate, glabrous above, tomentose to glabrate beneath, the primary veins 5–9 per side, the secondary veins reticulate, glabrous; inflorescences usually 1-flowered, tomentose to glabrate, the peduncle 0.5–2 cm. long, terminated by a pair of minute caducous bracts subtending a pedicel 3–15 mm. long; calyx ca. 11–16 mm. cleft ca. 0.33 of its length into free or connivent, valvate, acuminate lobes, usually lacerated below 2 sinuses, glabrate without, pilose within with ascending noncapitate hairs; corolla white, ca. 2-2.5 cm. long, cylindrical, cleft ca. 0.25 of its length into rounded, unequal, spreading lobes, glabrous without, with capitate hairs within; filaments ca. 2–3 mm. long, adnate opposite sinuses of anterior corolla lobe, bearing apically coherent anthers ca. 1 mm. below the corolla limb; staminodes 3, ca. 1.5 mm. long, adnate opposite posterior sinuses at middle of tube; cupulate annular disc conspicuous, 1 mm. high, deciduous; ovary and style ca. 8 mm. long, the ovary glabrous, the style with capitate hairs, separating 1–2 mm. above apex of mature ovary, the stigma applanate, bilobed, borne 6–7 mm. below the anthers; fruit white, ellipsoid, up to 25 mm. long and 8 mm. broad.

TYPE LOCALITY: Fiji, without further locality. Type collected by Horne, cited below.

DISTRIBUTION: Dense forest, interior mountains of central and northern Viti Levu, between 700 and 1,100 m.

LOCAL NAME: "Mimila" (*Smith* 4768).

FIJI: Without further locality, *Horne* 449 (K-lectotype), *Horne* 570–2 (GH, K). *Horne* 713 (GH).

VITI LEVU: Mba: Between Mount Vatuyanitu and Mount Natondra, Mount Evans Range, *Smith* 4304 (A, BISH, US); Mount Nairosa, eastern flank of Mount Evans Range, *Smith* 4412 (A-type of *Cyrtandra greenwoodiana* A. C. *Smith*., BISH, US); Mount Evans Range, *Greenwood* 1260 (A, US), 871–a (A); western slopes of Mount Nanggaranambuluta, *Smith* 4768 (A, BISH, US); Mount Nanggaranambuluta, *Greenwood* 871 (A, UC, US); *Gillespie* 3684 (BISH, UC); near Nandarivatu, *Gibbs* 572 (BM); *Degener* 14622 (A, BISH, NY, US), *Gillespie* 3385 (BISH, NY, UC, US), *Gillespie* 4038 (BISH, UC); Mount Matomba, Nandala, near Nandarivatu, *Degener* 14512 (A, BISH, NY, UC, US), 14833 (A, BISH, NY, UC, US). Namosi: Voma Mountain, *Gillespie* 2890.1 (UC).

Clarke's description is based on *Horne* 449, 570, and 1134 (not seen), all at Kew, of which *Horne* 449 is here designated as lectotype.

The relationship of this species is surely with *Cyrtandra esothrix*, and a tabular contrast of the two species is given under the latter. There is considerable intergradation in the leaves of these two species, and I know of no reliable means of distinguishing material in which flowers are not present.

25. Cyrtandra tavinunensis Gillespie, Bishop Mus. Bull. 74: 24, *fig. 33*, 1930.

Glabrous, slender shrub or small tree 3–4 m. high, the young stems with a flaky surface when dried; leaves opposite, the petioles 0.5–2 cm. long, the blades lanceolate to ovate, up to 20 cm. long and 6 cm. broad, equilateral and acute to attenuate at base, acute to acuminate at apex, undulate, glabrous above and beneath, with 5–7 upwardly curved primary veins per side, the secondary veins faintly to conspicuously reticulate beneath; inflorescences elongate, filiform, one-flowered, the peduncles up to 6 cm. long, bearing a pair of ovate, foliaceous bracts 10–12 mm. long, and 1–4 pairs of bracteoles, the terminal bracteoles subtending a pedicel ca. 3 cm. long; calyx ca. 8 mm. long, cleft ca. 0.33 of its length into 3–5 ovate, valvate lobes, glabrous on both surfaces; corolla greenish white, ca. 1 cm. long, cleft ca. 0.33 of its length into unequal lobes, the exterior glabrous, the interior with dense indument of papillate hairs ca. 100μ in diameter; filaments ca. 3 mm. long, adnate opposite the sinuses of the anterior corolla lobe ca. 5 mm. below the limb, bearing apically coherent anthers near the base of the limb; staminodes 2, adnate ca. 5 mm. below the limb; cupulate annular disc prominent, ca. 1 mm. high at anthesis, deciduous from maturing fruit: ovary and style glabrous, ca. 7 mm. long, the style separating near summit of the fruit; stigma applanate, bilobed, the lobes ca. 1.5 mm. long, ovate, borne below the anthers; fruit bright red, ovoid, up to 1.5 cm. long and 1 cm. broad.

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TYPE LOCALITY: Taveuni. Type collected by Gillespie, cited below.
DISTRIBUTION: Dense upland forests of Taveuni, 700–850 m.

TAVEUNI: Trail from Somosomo, *Gillespie* 4782 (BISH-type, NY, UC, US); summit and adjacent slopes of Mount Manuka, east of Wairiki, *Smith* 8234 (BISH, US).

The flaky surface of the young stems provides the most useful feature to distinguish *Cyrtandra taviunensis* from the closely related *C. montana*. This peculiar feature is not known in other Fijian species but does occur elsewhere in the genus, particularly in Malaysian species.

Further discussion of the relationship between this species and *Cyrtandra montana* is presented under the latter.

26. Cyrtandra montana Gillespie Bishop Mus. Bull. 74:22, *fig. 29*. 1939.
Cyrtandra bracteolosa A. C. Smith, Journ. Arnold Arb. 34:43. 1953.

Erect, glabrous shrub 2–5 m. high, the young foliage with indument of scattered, papillate hairs ca. 40μ in diameter, becoming glabrous at maturity; leaves opposite, the petioles 0.5–2.5 cm. long, the blades lanceolate to elliptic, up to 23 cm. long and 6 cm. broad, obtuse to acute to cuneate at base, acute to acuminate at apex, undulate to dentate, with 1–2 teeth per cm., glabrous above and beneath, 6–9 upwardly curved primary veins per side, the secondary veins faintly to conspicuously reticulate below; inflorescences filiform, glabrous, branching cymes, the peduncles ca. 1–3.5 cm. long, bearing a pair of deciduous, linear bracts 2–7 mm. long, the branches with 1–3 pairs of bracteoles, the terminal bracteoles subtending pedicels 0.5–3 cm. long; calyx 4–8 mm. long, glabrous on both surfaces, cleft ca. 0.5 of its length into ovate-acuminate, valvate lobes, the base slightly inflated; corolla white, broadly funnelform, up to 1.6 cm. long, cleft ca. 0.5 of its length into unequal, acute lobes, glabrous without, the limb within with indument of papillate hairs ca. 100μ in diameter, the throat within with short, capitate hairs ca. 30μ in diameter; filaments ca. 1.5 mm. long, bearing apically coherent anthers 1–2 mm. below the corolla limb; staminodes 3, ca. 0.5 mm. long, adnate ca. 3 mm. below the limb, the median staminode 1 mm. below the lateral; cupulate annular disc conspicuous, ca. 1 mm. high, deciduous; ovary and style glabrous, 5 mm. long, the style separating ca. 1 mm. above apex of mature fruit; stigma applanate, bilobed, borne ca. 2 mm. below the anthers; fruit orange to red, ovoid, up to 1.5 cm. long and 1 cm. broad.

TYPE LOCALITY: Wooded ridge on Naitarandamu Mountain, 1,100 m. Type collected by Gillespie, cited below.

DISTRIBUTION: Dense forests of Mba and Namosi, central Viti Levu, between 250 and 1,100 m.

VITI LEVU: Mba: Hills east of Nandala Creek, ca. 3 mi. south of Nandarivatu, *Smith* 6232 (A-type of *Cyrtandra bracteolosa* A. C. Smith, BISH, US). Namosi: Mount Naitarandamu, *Gillespie* 3144 (BISH-type, UC); Valley of Wainambua Creek, south of Mount Naitarandamu, *Smith* 8833 (BISH, US); hills north of Wainavindrau Creek, between Korombasambasanga Range and Mount Naitarandamu, *Smith* 8504 (BISH, US); northern slopes of Korombasambasanga Range, in drainage of Wainavindrau Creek, *Smith* 8732 (BISH, US).

A close examination of the types of *Cyrtandra montana* and *C. bracteolosa* has failed to reveal any differences that would justify the recognition of the latter as a distinct species. Smith (1953) indicated differences in the length of the calyx (4 to 5 mm. long in *C. bracteolosa* and 4 to 8 mm. long in *C. montana*), but a quantitative difference of this magnitude would be expected within a given species. The types were collected from the same general territory in the uplands of central Viti Levu.

The close relationship of *Cyrtandra montana* and *C. taviunensis* seems clearly indicated in their striking similarities in inflorescence, indument, flower structure, fruit size, fruit color, and other features. This lineage apparently does not extend into Polynesia, and there are no other currently known Fijian species that appear close to this remarkably distinctive pair. It seems reasonable to speculate that the two species were isolated by divergent, long-distance dispersal, probably by frugivorous birds attracted to the brightly colored fruits.

27. Cyrtandra pritchardii Seem. in Bomplandia 9: 257 (nomen), 364 (desc.). 1861; Fl. Vit. *t. 39.* 1866[4]

Cyrtandra coriacea C. B. Clarke, in DC. Monogr. Phan. 5: 280. 1883.

Cytandra gracilipes Gillespie, Bishop Mus. Bull. 74: 21, *fig.* 27. 1930.

Glabrous, freely branched shrub or small tree up to 5 m. high; leaves opposite, the petioles up to 2.5 cm. long, the blades lanceolate to elliptic, up to 18 cm. long and 5.5 cm. broad, equal to unequal and acute to cuneate at base, acute to acuminate at apex, undulate or entire, glabrous above and beneath, the primary veins obscure above, conspicious beneath, 8–12 per side, the secondary veins indistinct; inflorescences 1–3 flowered, the peduncles 0.5–1 cm. long on older branches, up to 2.5 cm. long on young shoots, terminated by a pair of caducous bracts ca. 0.5 mm. long, bearing 1–3 pedicels up to 2 cm. long; calyx coriaceous, 5–7 mm. long, cleft 0.33 of its length into 5 equal, valvate, lanceolate lobes, glabrous without, with capitate hairs within; corolla white, 1.5–1.8 cm. long, cleft ca. 0.33 of its length into unequal, rounded lobes, glabrous without, with capitate hairs within; filaments ca. 2 mm. long, adnate 3 mm. below the sinuses of the anterior corolla lobe, bearing apically coherent anthers at the base of the limb; staminodes 3, ca. 0.5 mm. long, adnate ca. 5 mm. below

[4] Also figured in Parham, Pl. Fiji Isl. *f. 87.* 1964.

the upper sinuses; cupulate annular disc prominent, ca. 0.5 mm. high at anthesis, drying to a fragmented, brown disc in mature fruit; ovary and style 9–12 mm. long, the ovary glabrous, the style with capitate hairs on upper 0.75 of its length, separating at summit or 2–3 mm. above apex of mature ovary, the stigma applanate, bilobed; fruit white, ellipsoid to fusiform, up to 2 cm. long and 1.2 cm. broad.

TYPE LOCALITY: Ovalau. Type collected by Seemann, cited below.

DISTRIBUTION: Dense forests of southeastern Viti Levu and Ovalau, between 50 and 500 m.

VITI LEVU: Serua: Hills west of Waivunu Creek, between Ngaloa and Korovou, *Smith* 9304 (BISH, US); hills between Waininggere and Waisese Creeks, between Ngaloa and Wainiyambia, *Smith* 9546 (BISH, US). Rewa: Summit of Korombamba Mountain, *Gillespie* 2393 (BISH); southeast slopes of Korombamba Mountain, *Gillespie* 2306 (BISH-type of *Cyrtandra gracilipes* Gillespie, UC), *Gillespie* 2221 (BISH, UC), Korombamba Mountain, *Meebold* 16726 (BISH); near Suva, *Horne* 698 (K-type of *Cytranda coriacea* C. B. Clarke), *Parks* 20068 (BISH, UC). OVALAU: "Mr. Pritchard's Estate," *Seemann* 283 (GH, K-type); without locality, *U.S. Expl. Exped.* (US).

The Ovalau specimens have broadly elliptic leaves, while the Viti Levu specimens have lanceolate to elliptic leaves; the material from the two islands seems similar in all other features. With no other differences to separate them other than slight contrasts in leaf shape, it seems best to refer *Cyrtandra coriacea* and *C. gracilipes* to *C. pritchardii*. This species was the first *Cyrtandra* to be described from Fiji; it is well illustrated in pl. 39 of Flora Vitiensis.

None of the Polynesian material I have examined bears any resemblance to *Cyrtandra pritchardii* but very similar material has been obtained from the Solomon Islands: San Cristoval, *Brass* 2690; and Guadalcanal, *Kajewski* 2711.

28. Cyrtandra denhamii Seem. Fl. Vit. 182. 1866.

Shrub or tree up to 5 m. high with rubiginose, septate, uniseriate, noncapitate hairs ca. 20μ in diameter and 0.25 mm. long; leaves opposite, glabrate at maturity, the petioles 1–3 cm. long, the blades lanceolate to elliptic, up to 19 cm. long and 6 cm. broad, unequal and obtuse to acute or cuneate at base, acute to acuminate at apex, undulate to dentate, with 1–3 teeth per cm., the venation conspicuous beneath, the primary veins 5–7 per side, the secondary veins reticulate; inflorescences many-flowered, branched, glabrate cymes, the peduncles 4–9 cm. long, terminated by a pair of deciduous, lanceolate to ovate bracts up to 1.5 cm. long, subtending braceteolate pedicels 0.5–3 cm. long, the bracteoles lanceolate, up to 6 mm. long; calyx white, deciduous, up to 1.5 cm. long, cleft nearly to base into 5 unequal, lanceolate, acuminate, valvate lobes, at maturity glabrate without, glabrous within; corolla white, 1 cm. long, cleft ca. 0.25 of

its length into unequal, rounded lobes, with capitate hairs ca. 40μ in diameter and up to 0.25 mm. long on both surfaces; filaments ca. 1 mm. long, bearing apically coherent anthers at the corolla sinuses; staminodes 3, 0.25 mm. long, adnate opposite the upper sinuses ca. 2 mm. below corolla throat, the median staminode about 0.5 mm. above the lateral; cupulate annular disc conspicuous, ca. 0.75 mm. high, drying to irregular rectangular fragments, persistent in mature fruit; ovary and style ca. 5 mm. long, the ovary glabrous, abruptly tapered to the style, the style with dense indument of capitate hairs, the stigma capitate, shallowly bilobed, the style separating 2–5 mm. above apex of mature fruit; fruit white, ellipsoid, up to 2.5 cm. long and 1.3 cm. wide.

TYPE LOCALITY: Mountains of Ngau, Fiji. Type collected by Milne, cited below.

DISTRIBUTION: Known only from the upland forests of Ngau, 300 to 450 m.

NGAU: "Mountains," *Milne* 236 (K-type); hills east of Herald Bay, inland from Sawaieke, *Smith* 7755 (BISH, US).

The type includes two specimens of which the lower specimen was annotated by Gray as a *Clerodendron*. However, my examination of the type reveals that the lower specimen is indeed *Cyrtandra denhamii*, as had been indicated by Seemann.

The deeply cleft calyx and sparse indument of the mature foliage characterize both *Cyrtandra denhamii* and *C. tempestii*. The eastward extension of this group into Polynesia is indicated by *C. feaniana* F. Brown, of the Marquesas Islands, and *C. longipedunculata* Rech., of Samoa, both of which have the inflorescence and flower characters of *C. denhamii*. The capitate, shallowly bilobed stigma of *C. denhamii* is unique among Fijian species of *Cyrtandra*, and also occurs in *C. feaniana*, cited above.

29. Cyrtandra tempestii Horne ex C. B. Clarke, in DC. Monogr. Phan. 5: 273. 1883.

Compact shrub or slender tree 3–4 m. high, with rubiginose tomentum on the younger parts, consisting of small, septate, uniseriate, noncapitate hairs ca. 15μ in diameter and 0.2 mm. long; leaves opposite, the petioles 5–6 cm. long, the blades ovate, up to 20 cm. long and 10 cm. broad, oblique and acute to obtuse at base, acute at apex, undulate to finely serrate at margin, at maturity glabrate above, glabrate to tomentose-sericeous beneath, the primary veins ca. 8–10 per side, the secondary veins reticulate; inflorescences many-flowered, branched cymes, the peduncles 0.5–1.5 cm. long, terminated by a pair of minute, caducous bracts subtending 2–4 branches, the pedicels 1–2 cm. long; calyx white, ca. 1 cm. long, cleft nearly to base into 5 equal, linear-lanceolate, valvate lobes, puberulent with

conspicuous, dark brown, noncapitate hairs without, glabrous within; corolla funnelform, white, ca. 2 cm. long, cleft 0.25 of its length into 5 unequal, reinform lobes to ca. 5 mm. broad, glabrous without, with capitate hairs within; filaments ca. 2 mm. long, adnate opposite the sinuses of the anterior corolla lobe, bearing apically coherent anthers ca. 3 mm. below the corolla limb; staminodes 3, 1–2 mm. long, adnate 1–2 mm. below filaments and opposite the posterior sinuses; cupulate annular disc conspicuous, ca. 1.5 mm. high, drying to a pelviform structure, persistent in mature fruit; ovary and style ca. 8 mm. long, glabrous, the style separating at the apex of the mature ovary, the stigma applanate, bilobed, borne ca. 4 mm. below the anthers; mature fruit white, ellipsoid, up to 1.6 cm. long and 1 cm. broad.

TYPE LOCALITY: Taveuni, "in woods near the sea at Na Seli Levie." Type collected by Horne, cited below.

DISTRIBUTION: Known only from two localities on Taveuni, where it occurs in dense forest at elevations from "near the sea" (*Horne* 1136) to 900 m.

TAVEUNI: East of Somosomo, near old crater occupied by small swamp and lake, *Smith* 8388 (BISH, US); Na Seli Levie, *Horne* 1136 (GH, K-type).

This species is closely related to *Cyrtandra denhamii* both in morphology and dispersal potential, for each species is of a lineage that has established populations in eastern Polynesia. The Polynesian populations related to *C. tempestii* occur on Rarotonga in the Cook Islands. These have the habit, leaves, inflorescence, calyx, and nectiferous annular disc of *C. tempestii*. The Cook Islands populations are currently recognized as a distinct species, *C. rarotongensis* Cheesm.

30. Cyrtandra ciliata Seem. (Bonplandia 9: 257. 1861, nom. nud.) Fl. Vit. 182. *pl. 41.* 1866.

Shrub to slender tree up to 4 m. high, the foliage with indument of septate, uniseriate noncapitate hairs ca. 30μ in diameter and up to 1 mm. long; leaves opposite, the petioles 2–6 cm. long, tomentose, the blades lanceolate to lanceolate-ovate or ovate, up to 28 cm. long and 12 cm. broad, oblique to inequilateral and rounded to acute or cuneate at base, acute to acuminate at apex, undulate to coarsely serrate, with ca. 2 teeth per cm., glabrous above, beneath glabrate to glabrous on the areoles, tomentose on the veins and margins, the primary veins 7 or 8 per side, the secondary veins reticulate below; inflorescences elongate, branching, many-flowered cymes with indument of non-capitate hairs ca. 20μ in diameter and 0.2 mm. long, the peduncles 0.5–5 cm. long, shorter in the inflorescences borne on older stems, terminated by caducous, linear bracts 1–2 mm. long, subtending bracteolate branches, the pedicels 1–5 cm. long; calyx green to white, deciduous, ca. 4 mm. long, cleft nearly to base into 5 equal, linear-lanceolate lobes with rounded apices, puberulent without, glabrous

within; corolla white, funnelform, ca. 2–2.5 cm. long, cleft 3–4 mm. into unequal, rounded lobes, with numerous capitate hairs without or glabrous, glabrous within; filaments ca. 3 mm. long, bearing apically coherent anthers at the base of the corolla limb; staminodes 3, ca. 1 mm. long, adnate ca. 4 mm. below the upper sinuses, the median staminode borne at same level as the lateral; cupulate annular disc prominent, ca. 1 mm. high, deciduous from the mature fruit; ovary and style ca. 1.5 cm. long, the ovary glabrous, the style with capitate hairs in upper half of its length, separating 1–4 mm. above the rounded apex of the mature ovary, the stigma applanate, shallowly bilobed, the lobes thick, spreading vertically; fruit white, ovoid, up to 12 mm. long and 7 mm. broad.

TYPE LOCALITY: Vuna, southwest Taveuni, Fiji. Type collected by Seemann, cited below.

LOCAL NAME: "Muskarimba" (*Smith* 1979).

DISTRIBUTION: Vanua Levu, Taveuni, and Koro, in dense forest, between 300 and 900 m.

KORO: Eastern slope of main ridge, *Smith* 965 (BISH, GH, NY, US). VANUA LEVU: Thakaundrove: Mount Mariko, *Smith* 435 (BISH, GH, NY, UC, US); Mount Ndikeva, *Smith* 1863 (BISH, GH, NY, UC, US); Natewa Peninsula, Uluingala, *Smith* 1979 (BISH, GH, NY, UC, US). TAVEUNI: Vuna, *Seemann* 282 (GH, K-type); between Somosomo and Wairiki, *Smith* 765 (BISH, GH, NY, US); Mount Manuka, east of Wairiki, *Smith* 8207 (BISH, US); without further locality, *Gillespie* 4724 (BISH, NY, UC).

The excellent plate in Flora Vitiensis has greatly facilitated identification, making this one of the most easily determined of the Fijian species. The affinities of *Cyrtandra ciliata* are not known. None of the other Fijian species have comparable flowers and inflorescences, and none of the Polynesian species are similar. It therefore seems likely that this species represents a lineage that is either peculiar to Fiji, or attenuated from Melanesian territory to the west, from which I have been able to examine very little material.

The variability in corolla indument is notable, for the populations from Vanua Levu are characterized by corollas with an outer indument of capitate hairs, while populations from Taveuni have corollas with a glabrous outer surface; however, the plants seem similar in other features. This difference is indicative of the propensity for evolutionary change in isolated populations of *Cyrtandra*. In such cases one has the alternative of either: circumscribing species to reasonably broad limits, or giving formal recognition to a number of separate, isolated populations, each distinguished by a slight morphological expression, such as the above.

31. Cyrtandra xanthantha A. C. Smith, Journ. Arnold Arb. 34: 48. 1953.

Shrub 3–4 m. high with ferrugineous, septate, uniseriate, noncapitate hairs ca. 30μ in diameter and to 1 mm. long; leaves opposite, the

petioles 1–3 cm. long, tomentose, the blades lanceolate to elliptic, up to 16 cm. long and 6 cm. broad, inequilateral and acute or cuneate at base, acute to acuminate at apex, entire to serrate, the serrations 1–2 per cm., papillate-puberulent to tomentose above, beneath densely tomentose with raised primary veins 6–8 per side and curved upwardly, the secondary veins reticulate beneath; inflorescences ferrugineous-tomentose, the peduncles 0.5–3 cm. long terminated by a pair of caducous, ovate-acuminate, connate bracts up to 1.7 cm. long and 0.8 cm. broad, the bracts villous above and below, subtending pedicels 0.5–1.5 cm. long; calyx deciduous, white to pale green, ca. 1 cm. long, cleft ca. 0.66–0.75 of its length into equal, lanceolate, valvate lobes, the tube and lobes villous without, glabrous within; corolla white to pale yellow, curved-cylindrical, up to 2.5 cm. long, cleft ca. 0.33 of its length into unequal, rounded, spreading lobes, the tube and lobes with capitate hairs without, glabrous within; filaments 2–3 mm. long, bearing apically coherent anthers at the base of the corolla limb; staminodes 2, ca. 1.5 mm. long, adnate near the middle of corolla tube; cupulate annular disc conspicuous, ca. 1 mm. high with irregular margin, deciduous in mature fruit; ovary and style 8–9 mm. long, the ovary glabrous, the style with capitate hairs in the upper half of its length, separating 1–2 mm. above the rounded apex of the mature ovary, the stigma applanate, shallowly bilobed, the lobes thick, spreading vertically, borne ca. 3 mm. below the anthers; fruit ellipsoid, up to 1.8 cm. long and 1 cm. broad.

TYPE LOCALITY: Slopes of the escarpment north of Nandarivatu, Fiji. Type collected by A. C. Smith, cited below.

DISTRIBUTION: Interior of Viti Levu in upland rain forest, 500–925 m.

VITI LEVU: Mba: Mount Evans *Greenwood* 376 (K); slopes of escarpment north of Nandarivatu, *Smith* 6277 (A-type, BISH, US); near Nandarivatu, *Gillespie* 4150 (A, BISH); valley of Singatoka River, near Nandarivatu, *Gillespie* 3979 (A, BISH).

The affinity of this species is with *Cyrtandra aloisiana*, and these two species do not appear to be closely related to other Fijian or Polynesian species. A tabular contrast of *C. xanthantha* and *C. aloisiana* is offered below:

	C. xanthantha	*C. aloisiana*
Habitat:	Montane inland rain forests 550–925 m.	Lowland coastal rain forests below 150 m.
Length of calyx lobes:	Lobes 2–3 times length of calyx tube.	Lobes 4–5 times length of calyx tube.
Inflorescence bracts:	Only outer bracts present.	Outer and inner bracts present.
Length of corolla:	Corolla up to 25 mm. long.	Corolla up to 10 mm. long.
Hairs of the petiole:	0.25–1.0 mm. long.	2–7 mm. long.
Staminodes	2, ca. 1.5 mm. long.	3, ca. 0.5 mm. long.

32. Cyrtandra aloisiana A. C. Smith, Sargentia 1: 116. 1942.

Shrub about 1 m. high with villous, rubiginose, septate, uniseriate noncapitate hairs ca. 60μ in diameter and up to 7 mm. long; leaves opposite, the petioles 1–5 cm. long, densely villous, the blades lanceolate to elliptic to ovate, up to 22 cm. long and 8 cm. broad, inequilateral and acute or cuneate at base, obtuse to acute or acuminate at apex, entire to faintly serrate, sparsely villous on the upper surface, beneath with villous pubescence and raised primary and secondary veins, the primary veins 6 or 7 per side; inflorescences congested, with 2–8 flowers, the peduncles 3–12 mm. long, terminated by a pair of caducous, lanceolate-ovate, acuminate, villous bracts up to 15 mm. long and 7 mm. broad, the bracts subtending bracteolate pedicels ca. 10 mm. long, the bracteoles up to ca. 7 mm. long and 3 mm. broad, deciduous, villous on both surfaces; calyx ca. 6 mm. long, deciduous, cleft nearly to base into 5 equal, lanceolate, acuminate lobes, these often connivent, villous without, glabrous within; corolla pale yellow, cylindrical, ca. 1 cm. long, cleft 2–3 mm. into unequal, erect, rounded lobes, the tube and lobes with capitate hairs without, glabrous within; filaments adnate ca. 2 mm. below the corolla throat, opposite sinuses of the anterior lobe, bearing apically coherent anthers at the base of the corolla limb; staminodes 3, ca. 0.5 mm. long, adnate near middle of the corolla tube; cupulate annular disc ca. 0.5 mm. high, conspicuous, with irregular margin, falling from the maturing fruit; ovary and style ca. 5 mm. long, the ovary glabrous, the style with indument of capitate hairs on upper 0.25 of its length, separating 2–3 mm. above the apex of the mature ovary, the stigma applanate, shallowly bilobed, the lobes thick, spreading vertically, borne 2–3 mm. below the anthers; fruit white, ellipsoid, 12–16 mm. long.

TYPE LOCALITY: Near Ngaloa, Serua, Viti Levu, Fiji. Type collected by Degener, cited below.

DISTRIBUTION: Forested slopes near the ocean, south coast of Viti Levu, 0–150 m.

LOCAL NAME: "Makamakandora" (*Degener* 15105); "Soronimbengga" (*St. John* 18952).

VITI LEVU: Nandronga & Navosa: Mbelo, near Vatukarasa, *Tabualewa* 15619 (A, BISH, UC, US); track north of Komave, *St. John* 18952 (BISH, US). Serua: Thulanuku, near Ngaloa, *Degener* 15105 (A-type, BISH, NY, UC, US).

This species and the closely related *Cyrtandra xanthantha* have no relationships to the Cyrtandrae of Polynesia insofar as I have been able to determine. The contrasts between *C. xanthantha* and *C. aloisiana* are presented under the former species.

33. Cyrtandra harveyi Seem. Fl. Vit. 182. 1866.
Cyrtandra gorriei Horne ex C. B. Clarke, in DC. Monogr. Phan. 5: 273. 1883.

Shrub 1–4 m. high with perfect or unisexual flowers and dark brown, septate, uniseriate, noncapitate hairs ca. 20μ in diameter and up to 0.5 mm. long, the pubescence dense and closely appressed on younger parts, sparse on mature foilage; leaves opposite, the petioles 2–9 cm. long, the blades lanceolate to ovate, up to 25 cm. long and 9 cm. wide, unequal and rounded to acute or cuneate at base, acute to acuminate at apex, serrate, above with appressed, upwardly directed parallel hairs, beneath with moderate to dense pubescence of spreading hairs; inflorescences bearing 1–3 flowers, the peduncles 3–15 mm. long, pubescent, very short and slender on older stems, longer and thicker on young shoots, terminated by caducous, lanceolate bracts 2–3 mm. long subtending pedicels 5–12 mm. long; calyx caducous, greenish white, fleshy, drying subcoriaceous, ca. 7 mm. long, cleft nearly half its length into 5 ovate to lanceolate, acuminate, free or connivent lobes, with 1 or more of the sinuses often lacerated, the tube and lobes with scattered, conspicuous, dark brown hairs without, glabrous within; corolla white, 2.5–3 cm. long, funnelform, slightly curved, and cleft ca. 0.125 of its length into rounded, unequal lobes, the tube and lobes with conspicuous capitate hairs ca. 30μ in diameter and 0.33 mm. long without, glabrous within; filaments of bisexual flowers ca. 8 mm. long and adnate 3 mm. below the sinuses of the anterior corolla lobe, bearing 2 apically coherent anthers in the broad corolla throat; staminodes 3, 1 mm. long, adnate ca. 7 mm. below the posterior sinuses, the median staminode borne ca. 1 mm. above the laterals; cupulate annular disc prominent, ca. 1 mm. high clasping a stalk, or gynophore ca. 1.5 mm. long, this expanding upward to the base of the ovary; ovary and style 1.7–2 cm. long, the ovary glabrous, the style with short, capitate hairs over its entire length, exserted 2–3 mm. above the corolla throat, separating 1–5 mm. above the apex of the mature ovary, the stigma applanate, shallowly bilobed; fruit white, ellipsoid, ca. 2 cm. long and 1 cm wide.

In female flowers (*Smith* 367, all cited specimens) both stamens and staminodes are absent and the style and ovary are 2–2.3 cm. long. The style is 1 mm. in diameter, much thicker than in bisexual flowers, and is exserted 3–4 mm. above the throat of the corolla.

TYPE LOCALITY: Nandi, Mbua, Vanua Levu, Fiji. Type collected by Harvey, cited below.

LOCAL NAME: "Merikula" (*Smith* 367).

DISTRIBUTION: Dense rain forests of Vanua Levu, between 100 and 400 meters.

VANUA LEVU: Mbua: Nandi, *W. H. Harvey*, s.n. (GH, K-type; Sandalwood Bay, *U.S. Explor. Exped.*, s.n. (GH, US). Mathuata: Southern base of Mathuata

Range, north of Natua, *Smith* 6761 (A, BISH, US); Wainunu-Ndreketi divide, *Smith* 1847 (BISH, GH, NY, US). Thakaundrove: Hills east of Mbalanga, Savu Savu Bay region. *Degener & Ordonez* 13899 (A, BISH, NY, UC, US); Vatunivu-amonde Mountain, Savu Savu Bay region, *Degener & Ordonez* 13969 (A, BISH, NY, UC, US); southern slope of Valanga Range, *Smith* 367 (BISH, GH, NY, UC, US); "mountains at Koro-ni-Saca" (near Nakuku), *Horne* 546 (K-type of *Cyrtandra gorriei* Horne ex C. B. Clarke).

The affinity of *Cyrtandra harveyi* clearly is with *C. coleoides*. Both species have distinctive morphological features not known in other Fijian Cyrtandrae. These include the peculiar stalk, or gynophore, at the base of the ovary, the exserted style, and the long (8–15 mm.), exposed filaments. The presence of gynodioecious flowers in this species is unique in Fiji; however, the occurrence of unisexual flowers in *Cyrtandra* is known in at least 16 species from New Guinea, 2 from Borneo, and 1 from Hawaii. Lauterbach placed the unisexual material in a separate genus, *Cyrtandropsis*, which Burtt (1936) considers untenable.

34. Cyrtandra coleoides Seem. (Bonplandia 9: 257. 1861, nom. nud.) Fl. Vit. 181, *pl. 40*. 1866.[5]
Cyrtandra alba Gilliespie, Bishop Mus. Bull. 74: 20, *fig. 25*. 1930.

Erect shrub or small tree 2–4 m. high with pruinose indument on younger parts, becoming glabrous at maturity; leaves opposite, the petioles 1–4 cm. long, the blades elliptic to ovate, up to 20 cm. long and 9 cm. wide, unequal to oblique and rounded to acute or cuneate at base, acute to rounded at apex, serrulate to undulate or entire, the primary veins raised beneath, 6–8 on each side of midvein; inflorescences borne on older, woody stems, glabrous, the peduncles ca. 1 mm. long, bearing deciduous bracts less than 0.5 mm. long, the bracts subtending 1–4 bracteolate pedicels, the bracteoles 0.5 mm. long, deciduous; calyx ca. 1 cm. long, parted or lacerated into irregular lobes, glabrous on both surfaces; corolla funnelform, ca. 2.5 cm. long, cleft 3–5 mm. into rounded, unequal lobes, the tube and lobes glabrous on both surfaces; filaments 10–12 mm. long, adnate 2–3 mm. below the sinuses of the anterior corolla lobe, bearing 2 apically coherent anthers above the throat; staminodes 2, 2.5 mm. long, adnate opposite the lateral sinuses at about the middle of the corolla tube; cupulate annular disc conspicuous, 1.5 mm. high, deciduous, flanged at base and constricted at rim, clasping a short stalk or gynophore ca. 1.5 mm. long, this expanding upwardly to the base of the glabrous ovary; ovary and style to 2.2 cm. long, at anthesis the ovary scarcely broader than the style, the upper half of the style with capitate hairs, separating at summit of the mature ovary, the stigma applanate, shallowly bilobed, presented above the throat and opposite the upper sinus but

[5] Illustrated in Parham, Pl. Fiji Isd. *f. 86*. 1964.

slightly below the anthers; fruit white, ellipsoid, up to 18 mm. long and 9 mm. wide.

TYPE LOCALITY: Namosi, Viti Levu, Fiji. Type collected by Seemann, cited below.

LOCAL NAME: "Makamakandora" (*St. John* 18227); "Lembalemba" (*Smith* 5628; "Mandiri tambua" (*Gillespie* 2671).

DISTRIBUTION: Dense upland rain forests of central and eastern Viti Levu, 150–1150 m.

VITI LEVU: Mba: Mount Tomanivi, *Smith* 5259 (A, BISH, US); hills between Nggaliwana and Nandala creeks, south of Nauwanga, *Smith* 5813 (A, BISH, US). Nandronga & Navosa: Northern portion of Rairaimatuku Plateau, *Smith* 5628 (A, BISH, US). Namosi: Voma Mountain, *Gillespie* 2671 (BISH-type of *Cyrtandra alba* Gillespie, UC), *Gillespie* 2924.1 (BISH); Wainavindrau Creek, near Wainimakutu, *Smith* 8879 (BISH), US; without further locality, *Seemann* 280 (GH, K-type). Naitasiri: Wainamo Creek, *St. John* 18227 (BISH, US). Rewa: Suva ditch trail, *Bryan* 378 (A, BISH).

It has not been possible for me to find a morphological basis for separating *Cyrtandra alba* from *C. coleoides*. The types of both species were collected in the province of Namosi, Viti Levu. The type of *C. alba* was collected on Voma Mountain, Namosi. It is known that Seemann collected on the same mountain so that the locality information as well as available morphological comparisons support the reduction of *C. alba* to synonymy under *C. coleoides*. Gillespie's illustration of *C. alba* incorrectly portrays the calyx with 5 equal lobes. The type material clearly has the calyx lacerated into irregular segments as in *C. coleoides*, and a pencil sketch attached to the type of *C. alba*, obviously the basis for the published illustration, portrays the calyx with lacerated, irregular segments. There is obviously a close relationship between this species and *Cyrtandra harveyi*. The morphological comparisons of these two species are presented under the latter.

35. Cyrtandra prattii Gillespie, Bishop Mus. Bull. 74: 24, *fig. 32*. 1930.

Erect shrub up to 3 m. high, the ligneous branches to ca. 2 cm. in diameter, the pith scanty, up to 1.5 mm. in diameter, the young foliage tomentose with septate, uniseriate, noncapitate hairs ca. 50μ in diameter and 0.75 mm. long, becoming glabrate to glabrous at maturity; leaves opposite, the petioles 1–3.5 cm. long, the blades lanceolate to elliptic, up to 20 cm. long and 8 cm. broad, acute to cuneate at base, acute to acuminate at apex, faintly serrate, with 1–2 serrations per cm., at maturity glabrate to glabrous above, densely pubescent to glabrate beneath, the primary veins raised beneath, curved upward, 6–9 per side, the secondary veins conspicuously reticulate beneath; inflorescences with an elongate, woody axis to 35 cm. long, arising in the lower part of stem or at ground level among the adventitious

roots, bearing at 1–3 cm. intervals ovate, connate-perfoliate, deciduous bracts 0.5–1 cm. long, the bracts glabrate without, pilose within, subtending tomentose pedicels 3–7 mm. long; calyx ca. 2 cm. long, cleft ca. half its length into unequal, lanceolate, acuminate, sometimes connivent lobes, often lacerated nearly to base below the anterior sinus, densely tomentose on both surfaces; corolla pale yellow, cylindrical, fleshy, drying coriaceous, ca. 3 cm. long, cleft to 0.33 of its length into unequal, rounded lobes, the tube and lobes tomentose without, glabrous within; filaments 2–3 mm. long, bearing apically coherent anthers ca. 1 mm. below the corolla limb, the anthers black, apiculate, ca. 2 mm. long; staminodes 2, ca. 0.5 mm. long, adnate opposite posterior sinuses ca. 5 mm. below the limb; cupulate annular disc conspicuous, ca. 1.5 mm. high, deciduous in mature fruit; ovary and style ca. 2 cm. long, densely tomentose with noncapitate hairs ca. 40μ in diameter and up to 1 mm. long, the stigma applanate, bilobed, the lobes ovate, ca. 4 mm. long, with inner pubescence of capitate hairs ca. 20μ in diameter and ca. 0.1 mm. long, the style separating ca. 3 mm. above apex of mature ovary; fruit white, ovoid, ca. 2 cm. long and 1.2 cm. broad.

TYPE LOCALITY: Near summit of Mount Tomanivi, Mba, Viti Levu, Fiji. Type collected by Gillespie, cited below.

DISTRIBUTION: Dense upland forests of central Viti Levu, 900–1300 m.

LOCAL NAME: "Andalunga" (*St. John* 18260).

VITI LEVU: Mba: Mount Tomanivi, *Gillespie* 4091 (BISH-type, UC). Naitasiri: Wainamo-Wainisavulevu Divide, Rarandawai, *St. John* 18260 (BISH, US). Fiji, without further locality, *Parks* 20242 (BISH).

No likeness to this species has been seen in other Fijian Cyrtandrae, nor in the Polynesian material. The unique inflorescence surely justifies the assignment of this species to a distinct group among the Fijian species of *Cyrtandra*. The closest relationship of *Cyrtandra prattii* would appear to be with *C. nodosula* Schlecht., of New Guinea.

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Camissonia brevipes (A. Gray) Raven subsp. *brevipes*, from a watercolor by Henry R. Mockel, made near Palm Springs, Riverside County, California; original in the Hunt Botanical Library, Pittsburgh. Reproduced by permission of Mr. Mockel and the Hunt Botanical Library.

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A REVISION OF THE GENUS CAMISSONIA (ONAGRACEAE)

By PETER H. RAVEN

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A REVISION OF THE GENUS CAMISSONIA (ONAGRACEAE)

By Peter H. Raven

Introduction

Camissonia is one of the better characterized genera of Onagraceae' tribe Onagreae. This tribe consists of 11 genera, more than half of the total for the family. Included in it are some 215 species, comprising about a third of the Onagraceae. My most recent synopsis of the genera and tribes of the family was presented in 1964 (Brittonia 16: 276) and listed 12 genera of Onagreae. Subsequently, a detailed study of the then monotypic genera *Gongylocarpus* and *Burragea* (Carlquist and Raven, Amer. Journ. Bot. 53: 378–390. 1966) has led to the conclusion that they should be merged. I would now list the genera of the tribe Onagreae as follows: *Gongylocarpus* (including *Burragea*), *Camissonia, Gayophytum, Xylonagra, Oenothera, Stenosiphon, Hauya, Calylophus, Gaura, Clarkia, Heterogaura.*

I cannot agree with Munz (N. Amer. Fl. II. 5: 53. 1965) as to the desirability of separating *Hauya* as a tribe distinct from the rest of the Onagreae solely because these plants have stipules. This appears to be an unwarranted emphasis of a single characteristic which would lead to a less realistic portrayal of affinities within the family. Indeed, the evidence seems to indicate clearly that *Hauya* is more closely related to the other genera of tribe Onagreae with divided sporogenous tissue—*Calylophus, Gaura, Clarkia,* and *Heterogaura*—than these genera are to the remainder of the tribe. It scarcely seems credible that the division of the sporogenous tissue of the anthers into packets, separated by sterile tissue, is a characteristic that arose more than once in the evolution of this group, and the combination of evening opening of the flowers (in *Hauya, Calylophus hartwegii* sens. lat., and most species of *Gaura*) with a broad, open hypanthium can hardly be dismissed as mere coincidence.

My own work on the genus *Camissonia* was initiated in August 1957 and has occupied much of my time since that date. It is based on the rich collections of this genus in the herbarium of the United States National Museum and other herbaria (listed below), as well as on extensive field studies throughout the area of the group. The first

part of this work was published in 1962—a revision of the group then known as *Oenothera* subg. *Chylismia* (Univ. Calif. Publ. Bot. 34: 1–122). Subsequently, I became convinced that the species recently included in *Oenothera* could better be grouped as three genera: *Camissonia*, *Calylophus*, and *Oenothera*. I explained the reasons for this decision to Dr. Philip A. Munz, and he requested that I publish this material in synoptical form so that he could adopt the new generic delimitations for his forthcoming treatment of the family (N. Amer. Fl. II. 5: 79. 1965). Setting aside my work on the present revision, I prepared a synopsis of the species and the sectional classification of *Camissonia*, making new combinations when names were available and in general presenting a bare outline of my views on the species in this group, but without detailed justification. I did not, however, publish any new species for which names at some level were not already available. I made this manuscript available to Dr. Munz and proceeded to get the material into print as soon as possible (Brittonia 16: 276–288. 1964).

Soon after the article appeared, Dr. Munz informed me that he had changed his mind and would not accept my concepts of the genera involved. He did, however, accept every proposition I made about species, subspecies, and sections, making some dozens of transfers of these taxa to *Oenothera* without comment on or justification for their new status. I would naturally have preferred to make these changes in rank in the present paper, where they could be fully discussed and justified in detail. I have attempted to do this herein, even when the changes in status have been made earlier.

Delimitation of *Camissonia*

In order to evaluate the position of *Camissonia*, it is necessary to review some of the material I presented in 1964. *Clarkia*, recognized as a distinct genus by all authors for more than 50 years, is distinguished from *Oenothera* (in the broad sense of Munz) by two characteristics only: its possession of divided sporogenous tissue in the anthers and by the basal attachment of these anthers. But similarly divided sporogenous tissue is found in *Hauya*, *Gaura*, *Heterogaura*, and in that portion of *Oenothera* treated by Munz as the subgenera *Calylophus* and *Salpingia* and by me as the genus *Calylophus*. All of these genera are likewise similar in stigma morphology (Raven, Brittonia 16: 278. 1964) and in their broad, relatively long hypanthia. The evidence that they are a coherent group, with clear interrelationships, appears unequivocal.

There are two other distinctive groups of genera in the tribe Onagreae. The first consists of *Oenothera* (in the relatively narrow sense) and *Stenosiphon*, separated most obviously by the indehiscent,

1-seeded fruits of the latter. In these two genera, the stigma is of a type unknown elsewhere in the family: 4-lobed, without any disc at the base and the lobes receptive all around. The second group consists of the genera *Gongylocarpus*, *Xylonagra*, *Gayophytum*, and *Camissonia*, all consisting of plants with a capitate or hemispherical stigma of a sort widespread in the rest of the family, as well as relatively short hypanthia and flowers that open primarily in the morning.

Looking at the pattern of variation in the tribe from this vantage point, it is possible to recognize three distinct groups, the relationships between which are not close. In spite of its highly specialized fruits, it seems clear that *Gongylocarpus* includes the most generalized species found in the tribe. It is the only genus of the tribe that retains the original basic chromosome number for the family, $n=11$. It is further clear that the sort of capitate or hemispherical stigma found in this genus and in *Xylonagra*, *Gayophytum*, and *Camissonia* is primitive in the tribe and probably in the family as a whole. One other genus of the tribe, *Hauya*, has a similar hemispherical stigma; but in *Hauya*, as we have seen, the sporogenous tissue in the anthers is divided into packets by sterile tissue. *Hauya* is generalized in a number of respects: chromosome number ($x=10$), habit (shrubs or trees to more than 30 m. tall), and possession of stipules. Thus *Hauya* must represent a relatively early offshoot of the phyletic line that also gave rise to *Calylophus*, to *Gaura*, to *Clarkia*, and to *Heterogaura*. One could scarcely imagine that these groups gained their identical anther morphology independently, and we have mentioned their similar floral morphology and biology. The relationships of the group comprising *Oenothera* and *Stenosiphon* are obscure, although is it clear that they belong in the tribe Onagreae. At some point the ancestors of these plants made the transition to an evening-opening habit, with the deep, narrow hypanthia and expanded stigmatic surface characteristic of moth-pollinated plants in many families.

What then is the rationale for retaining *Oenothera*, *Camissonia*, and *Calylophus* in a single genus, when these three groups differ absolutely in anther morphology and stigma morphology, and modally in floral biology? At best, this can be justified only on historical grounds; there are no transitions between these three groups, no species are intermediate, and no confusion of delimitation exists. The characters used to separate the universally recognized genera *Clarkia*, *Gayophytum*, *Stenosiphon*, *Gaura*, *Heterogaura*, and *Xylonagra* are of the same sort as those which separate *Oenothera*, *Camissonia*, and *Calylophus*, and the groups delimited are clearly as meaningful and coherent phenetically. Of even more crucial importance, the evidence that these three genera are each more closely related to other genera than they are to one another appears overwhelming; not a single fact

has been adduced in opposition to this view. If our taxonomy is to show anything whatsoever about the relationships of plants, there appear to be only two possible courses of action. One would result in the grouping of all genera of the tribe Onagreae, except *Hauya* and *Gongylocarpus*, into a single genus; the other is the generic treatment adopted here.

Historical and Taxonomic Considerations

A historical review of generic concepts in the tribe Onagreae was presented in 1964 (Raven, Brittonia 16: 276–288) and will not be repeated here. Many aspects of the taxonomic history of particular species groups are given in the general remarks on the sections concerned. A few general points are, however, germane.

The genus *Camissonia*, as delimited in this treatment, was first outlined in my 1964 paper. Indeed, *Camissonia* is a somewhat unfamiliar name, *Sphaerostigma*, *Taraxia*, *Eulobus*, and *Chylismia* being more frequently employed at the generic level for some of its constituent groups. Very few combinations under *Camissonia* were made prior to 1964; nevertheless, this does clearly seem to be the oldest generic name applied to the complex in question, antedating *Sphaerostigma* by 17 years. Although the name *Sphaerostigma* is more familiar, it has never been used in the inclusive sense of *Camissonia* as applied in the present monograph, and nothing seems to be gained by conserving it or any other junior synonym over *Camissonia*.

Most species of *Camissonia* are endemic to the Western United States, with three reaching adjacent Western Canada, a number in the bordering states of Mexico, and one in Western South America, whence the first known species, *C. dentata*, was described by Cavanilles in 1795. The increasing tempo of exploration of California and adjacent regions throughout the 19th century led to the discovery of most of the species known today. The first more or less synoptical treatment was that of Sereno Watson in his "Revision of the extratropical North American species of the genus *Oenothera*" (Proc. Amer. Acad. 8: 573–618. 1873); Watson's work was reasonable and conservative as to species delimitation. In 1896, John Kunkel Small published a review of the species under the title, "*Oenothera* and its segregates," Bull. Torrey Cl. 23: 167–194. 1896. This was an exceedingly uncritical treatment at both specific and generic levels, replete with new combinations and hasty, superficial judgments. Starting six years later, Hector Léveillé confused the taxonomy of *Oenothera* and related groups to an unprecedented degree by publishing his "Monographie du Genre *Onothera* (1902–1913)." Léveillé was surely one of the most erratic taxonomic workers ever to publish a large amount of material, and it is unfortunate that he concentrated so

much of his effort on *Oenothera*; his illustration of an annual member of the Polygonaceae, facing p. 167 of his Monographie, labeled "*Onothera gracilis* (Philippi) Lévl." is merely one example of his notoriously superficial work. Aven Nelson remarked about Léveillé's efforts in 1905 (Bot. Gaz. 40: 54. 1905), "It is extremely difficult to believe that his grouping of the specimens can stand, especially when one finds that the annotations do not harmonize with the final published list, and that the nomenclature of the illustrations in some instances does not coincide with that of the text."

Nelson did not help matters much in his review of *Sphaerostigma*, presented as "Contributions from the Rocky Mountain Herbarium. VI." (Bot. Gaz. 40: 54–63. 1905), for this was again a relatively uncritical listing of species which did not advance the understanding of the group to any marked degree. On the other hand, this paper did, for the first time, have the advantage of some knowledge of the plants in the field, and it probably represents an improvement over the efforts of Small and Léveillé, if not those of Watson.

In 1928, when P. A. Munz instituted his invaluable monographic series on *Oenothera*, there were probably few groups of plants in the United States for which the taxonomy was more confused. The conservative approach used in Munz' revisions of *Oenothera* subg. *Chylismia* (Amer. Journ. Bot. 15: 223–240. 1928), *Sphaerostigma* (Bot. Gaz. 85: 233–270. 1928), and *Taraxia* and *Eulobus* (Amer. Journ. Bot. 16: 246–257. 1929) brought a remarkable degree of order out of a tremendously confused situation. These three papers provided a sound basis for the accumulation of knowledge about the plants here treated as *Camissonia* which has served very well for some 40 years.

It is instructive to consider how and why the present revision differs from them. Munz recognized 32 species; the present paper includes 61. Both, coincidentally, recognize 29 major infraspecific taxa. Thus the number of species has nearly doubled in the 40 years. One obvious reason for this change has been the accumulation of additional herbarium material during the intervening years. In 1929 Munz had available 13 collections of the three species of sect. *Eulobus* endemic to Baja California; I have been able to study well over a hundred. That this has not been the primary reasons for the recognition of more species, however, is suggested by the fact that in this section, for all the accumulation of additional information, the taxonomy has remained unchanged.

A much more important reason for the recognition of more species now than in 1928–9 has been the accumulation of additional information. First has been chromosomal information so vital to an understanding of the polyploid complexes which sect. *Holostigma* and sect. *Camissonia* have proved to be. It is not surprising that some of the

most dramatic inflations in species number have taken place in these groups, 4 species and 7 additional varieties in the former being recognized here as 14 species with 3 additional subspecies, and 2 species with 6 additional varieties in the latter being recognized here as 12 species with 4 additional subspecies. These changes have been made largely to accommodate the distinctive population systems that have been revealed by chromosomal information, although a few of the taxa recognized were unknown or uncollected in 1929. A second sort of information concerns the breeding systems of the plants concerned; thus series of populations consisting of relatively large-flowered, often self-incompatible individuals are routinely separated at present from their relatively small-flowered, autogamous relatives at the specific level, whereas in 1929 the biological significance of such distinctions was largely unknown to or not appreciated by taxonomists.

The most important changes in taxonomy in the past 40 years, however, have been philosophical. In 1929, degree of difference or similarity was the aspect of variation patterns stressed most in making taxonomic decisions. In 1968, the pattern itself was stressed, with discontinuities in the pattern of variation being emphasized as much as or in some instances even more than the degree of similarity between the two populations being compared. In 1929 relatively similar populations were often grouped as varieties of a single species regardless of whether they intergraded or remained completely distinct in nature. Very different plants were separated at the species level even if they intergraded completely and numerous intermediates were represented in the material being studied. The taxon here called *Camissonia pubens* was formerly considered a variety of *Oenothera contorta* (Munz, Bot. Gaz. 85: 254. 1928), even though no intermediates were found or expected; on the other hand, the taxa here called *Camissonia boothii* subsp. *desertorum* and subsp. *alyssoides*, being quite different, were considered to belong to distinct species, even though it was noted that the former "grades . . . insensibly . . ." (Munz, Bot. Gaz. 85: 246. 1928) into the latter. Neither treatment reflects more information about the systems of populations being classified, or is "better"; rather, each is in accordance with the taxonomic spirit of the times in which it was constructed. As usual, one must turn to the presentation of data on which the taxonomy is based to learn anything about the pattern of variation that underlies the taxonomy; the mere recognition of taxa conveys only a strictly limited amount of information about the organisms being classified. Either sort of taxonomic philosophy might be used to construct a useful classification if the facts on which it was based were correct and well ordered; neither could be so used if the facts were incorrect or poorly aligned with one another. In the final analysis, all one can ask of a taxonomic system is that the popu-

lations classified as lower level taxa be more similar to one another (in some respect) than are the populations classified as higher level taxa. Thus one would logically expect two subspecies to be more similar to one another than two species in the same group; whether this is true or not will depend on the perceptiveness of the taxonomist making the classification and on the information available to him.

There is more unanimity about another philosophical difference between the taxonomy of 40 years ago and the taxonomy of the present. In 1929, it was considered quite acceptable to give names to infraspecific taxa which were based on genetically different members of Mendelian populations, providing that one wished to emphasize the differences between them. The denial of John Ray's 17th-century dictum about the construction of taxa implicit in the taxonomic recognition of such segregating entities went largely undetected until the 1930s, when populations and not individuals were clearly established as the units of biological classification. In general, taxonomists intentionally have not given different formal names to the progeny of a single individual or pair of individuals, no matter how different these might be, and this has been the prevalent tradition for some 300 years. In part, of course, the recognition of such entities as varieties sometimes happens when insufficient information is available; but in the 1920s such a taxon as *Oenothera cheiranthifolia* var. *nitida* could be recognized as distinct, basically because "the aspect of a wholly glabrous plant is quite different from that of a very hairy one . . ." (Munz, Bot. Gaz. 85: 270. 1928), even though such plants were well known to occur as segregating elements in normal populations. Most taxonomists would not at present accord formal recognition to such an entity.

The desire to give formal taxonomic names to distinct populations only and not to the genetically distinctive elements in such populations underlies the modern preoccupation with the geographical race as the only infraspecific entity worthy of recognition, a tendency that was apparent more than a century ago. Many taxonomists of the present day formally recognize only geographic races below the species level, although this may sometimes pose difficulties when the organisms being classified are largely or wholly autogamous.

Subspecies are used herein as the only infraspecific taxon for the following reasons. The Code states explicitly that subspecies are the primary unit into which species are divided, and it is therefore incorrect to use any other infraspecific taxon, such as variety, for the primary division of a species. From a formal standpoint, there is much to recommend Pennell's (Amer. Journ. Bot. 36: 1922. 1949) suggestion to treat subspecies and varieties as synonymous, to use the former word in scientific nomenclature and to relegate the latter

to informal usage, where the term "variety" has already gained a multiplicity of meanings quite inconsistent with its employment as a scientific term. Should such a suggestion be adopted, the nomenclatural problem would be simplified and the number of new combinations greatly reduced. A tendency toward the recognition of only one level of taxa below the level of species is already apparent in Europe. For me, the recognition of more than one such level implies a degree of precision in the understanding of relationships which often becomes ludicrous. As H. L. Mason has often emphasized, two of any three taxa will always be more closely related to one another than they are to the third; but is it practical to recognize all such shades of relationship in our formal taxonomy, even if it were possible to ascertain the facts of the case unequivocally? I personally feel that the adoption of the trinomial system in zoology at an early date was a sound solution of this particular problem of nomenclature. I hope that botanists may ultimately adopt such a system and consider it desirable meanwhile for names at both varietal and subspecific levels to be considered for purposes of priority at either one, even though it is not technically necessary to do so.

In the present revision, I have tried to indicate in the synonymy how the concepts of Munz can be integrated with my concept. I have not given references to other taxonomic papers, since this has been done by Munz in his revisions, which have been the only important basis of classification of the groups for some 40 years. I have, however, given full synonymy and citation of types in all cases. Specimens are not cited here for many of the taxa treated in the same sense in which they were understood by Munz; the ranges of such taxa are already sufficiently documented in the literature. For sects. *Chylismia*, *Lignothera*, and *Chylismiella* I have not cited specimens or given distribution maps, since this information has been presented in my earlier revision (Raven, Univ. Calif. Publ. Bot. 34: 1-122. 1962).

Geographical Distribution

Camissonia is primarily a group of the Western United States and adjacent Mexico, although a few autogamous species extend beyond this area. Three species—*Camissonia andina*, *C. breviflora*, and *C. contorta*—are found in the southern part of Western Canada; all of them are autogamous. On the other hand, 79 of the 90 taxa recognized in this revision are found in California, and 21 are endemic to the State (12 other endemics just reach southern Oregon or northwestern Baja California). Three of the four species of *Camissonia* sect. *Eulobus* are endemic to Baja California, as are *C. cardiophylla* subsp. *cedrosensis* (technically also found in Sonora because of its

occurrence on Isla Tiburón), *C. claviformis* subsp. *wigginsii*, *C. proavita*, and *C. guadalupensis* subsp. *guadalupensis*, the last two in the California floristic region. No taxon is endemic to Sonora, although eight occur there, and *C. californica* and *C. chamaenerioides* range widely in the State. No species of *Camissonia* is known from Chihuahua, although *C. chamaenerioides*, the only species of the genus that occurs in Texas, may well occur there. Only two species, *C. chamaenerioides* and *C. scapoidea* subsp. *scapoidea*, are definitely known to occur in New Mexico, although *C. refracta* may also occur in that State.

In Arizona, 27 taxa occur, and *C. palmeri* and *C. strigulosa* might also be represented. Of these, *C. claviformis* subsp. *peeblesii*, *C. speculicola* subsp. *hesperia* and subsp. *speculicola*, *C. confertiflora*, *C. scapoidea* subsp. *macrocarpa*, and *C. exilis*, all belonging to sect. *Chylismia*, are endemic. In Colorado, only *C. walkeri* subsp. *walkeri*, *C. eastwoodiae*, and *C. scapoidea* subsp. *scapoidea* of sect. *Chylismia*, *C. parvula* of sect. *Camissonia*, and *C. breviflora* and *C. subacaulis* of sect. *Tetrapteron* are known, and only *C. scapoidea* occurs east of the Rocky Mountains. Utah has 22 taxa, none endemic, and Nevada has 33, with *C. nevadensis* and *C. megalantha* well-marked endemics. In Wyoming, *Camissonia scapoidea* subsp. *scapoidea*, *C. subacaulis*, *C. breviflora*, *C. parvula*, *C. minor*, and *C. andina*, all autogamous, are found, with only *C. subacaulis*, *C. breviflora*, and *C. andina* reaching Montana. Idaho has 13 taxa, Oregon 18, and Washington 10; *Camissonia hilgardii* is virtually endemic to Washington and *C. pygmaea* endemic to the 3-State area.

It is evident, therefore, that *Camissonia* centers in the California floristic area, where the plants chiefly occur in plant associations derived from the Madro-Tertiary Geoflora. Sect. *Holostigma*, with 14 species and 3 additional subspecies, is virtually endemic to this region, as is the close-knit group of 11 taxa comprising species 44–51 of sect. *Camissonia* (this latter group also including the only South American species, the autogamous *C. dentata*). Two other sections (*Chylismia* and *Eremothera*) and the four taxa comprising species 40–43 of sect. *Camissonia* center in the Great Basin and adjacent deserts to the south, as does the monotypic sect. *Chylismiella*. Sect. *Nematocaulis*, comprising two closely related species, is associated with the high, cold deserts north of the Great Basin, and sect. *Tetrapteron*, while probably radiating from floristic regions similar to those represented in cismontane California at the present day, has also radiated in the mountains and deserts of these northern regions. Sect. *Lignothera* has its maximum diversity in the deserts and mountains about the head of the Golfo de California. Finally, sect. *Eulobus*, small but phylogenetically crucial, is primarily associated with the peninsula of Baja

California, well known as one of the most important refugia in the southern part of North America, where it is associated with *Gongylocarpus fruticulosus* (Benth.) T. S. Brandegee, perhaps the most generalized species of the tribe Onagreae surviving at the present day.

Phylogenetic Relationships

In the light of information presented up to this point, what can be said about the relationships of the sections of *Camissonia?* First of all, the nine sections I have recognized are sharply distinct from one another, and there are no transitions between them. Their association into phylogenetic lines or circles of affinity is extremely problematical, and there seems to be absolutely no advantage to be gained by grouping them into subgenera as has been done by Munz (N. Amer. Fl. II. 5: 142–177. 1965); indeed, I would hold that such an association of the sections into artificial groupings is misleading. *Camissonia* is clearly the most heterogeneous of the 11 genera of the tribe Onagreae, and its sections are amply differentiated. Keeping these facts in mind, it is possible to offer a few deductions about the phylogeny of the group and the relationships of its constituent parts.

We have already seen that the genus *Gongylocarpus* comprises the most generalized species in the tribe, and it appears reasonable to use it as a standard for examining phylogenetic relationships in *Camissonia*. The other two genera closely related to *Camissonia*—*Xylonagra* and *Gayophytum*—do not appear to offer much guidance in this respect; although, as we shall see, the restriction of the monotypic *Xylonagra* to central Baja California may well be significant. Within *Gongylocarpus*, the low shrub *G. fruticulosus* is clearly more generalized, in view of its self-incompatibility, woody habit, and large flowers, than the wide-spread autogamous *G. rubricaulis* Schlecht. & Cham. (Carlquist & Raven, Amer. Journ. Bot. 53: 378–390. 1966). *Gongylocarpus fruticulosus* is restricted to two adjacent islands in Bahía Magdalena, southern Baja California, where it is locally abundant.

Geographically, it is clear that *Camissonia* sect. *Eulobus*, the only section of the genus centering in Baja California, where three of its four species are endemic, deserves special attention. One of its species, *Camissonia crassifolia*, has the woodiest habit of any *Camissonia*; also the section shares with *Gongylocarpus* the fleshy disc within the hypanthium which is, among the members of tribe Onagreae, known only in these two genera. Thus the woody habit, the fleshy disc in the hypanthium, and a common habitat in the Baja California littoral all link *Gongylocarpus fruticulosus* with *Camissonia crassifolia*, and I believe the latter to be the most generalized extant species of its genus.

Within *Camissonia*, pinnately lobed or divided leaves are found only in sect. *Eulobus*, sect. *Chylismia*, and sect. *Tetrapteron*, and the members of the latter group are the only species of *Camissonia* which share with sect. *Eulobus* a fleshy disc closing the hypanthium. The relationship between *Eulobus* and *Chylismia* is obviously close; indeed, the basal rosette of *Camissonia californica* (which normally withers by the time the plants flower) is often virtually indistinguishable from that of *C. multijuga*, one of the more generalized species of sect. *Chylismia*. One of the most interesting lines of evidence for a close relationship between these three groups, however, has been developed recently; in some species of each most of each petal is strongly ultraviolet reflective, as usual in the genus, but the basal portion is occupied with a conspicuous, nonultraviolet-reflecting spot which is invisible to the human eye but can be photographed with special techniques (D. P. Gregory and P. H. Raven, MS.). No such nonultraviolet-reflecting areas have been found on the petals of outcrossing species of sect. *Holostigma*, sect. *Camissonia*, or sect. *Eremothera*, and in the first two examples, the place of this nonultraviolet-reflecting spot is obviously taken by the one or two large, bright brownish-red dots at the base of each petal, which doubtless serve the same function as nectar guides. The species of sects. *Chylismia* and *Tetrapteron* that have the nonultraviolet-reflecting spots have petals that appear clear, bright yellow and unspotted to the human eye, whereas those of sect. *Eulobus* have a distinctive, fine red flecking throughout the nonultraviolet-reflective area.

In summary, I hold that sect. *Eulobus* is the most primitive group within the genus *Camissonia*, and that from plants similar to this group were derived the ancestors of sect. *Chylismia*, which radiated into the deserts and later gave rise to the small section *Lignothera*, specialized for pollination by hawk moths. Also from plants similar to sect. *Eulobus*, the species of sect. *Tetrapteron*, which became associated with more mesic habitats, were derived. Presumably among the most primitive species of sect. *Holostigma* is *Camissonia cheiranthifolia*, the only woody or even perennial species found among the last five sections of the genus as I have arranged it here. These sections were probably also derived from plants similar to those of sect. *Eulobus*. All species of these five relatively advanced sections have simple leaves that are never lobed (at the most coarsely serrate); none has a disc in the hypanthium; and none has a nonultraviolet-reflective area on the petal, so far as known.

Evident shifts from the perennial to the annual habit have characterized the first five sections listed here (the last four are strictly annual); these shifts have usually been accompanied by a change

from self-incompatibility to self-compatibility. Self-incompatible species are distributed among the nine sections of *Camissonia* as follows:

	Self-incompatible species	*Self-compatible species*	*Total*
I. *Eulobus*	2	2	4
II. *Chylismia*	[a] 7	6	13
III. *Lignothera*	–	2	2
IV. *Tetrapteron*	[b] 2	[c] 4	6
V. *Holostigma*	[d] 2	12	14
VI. *Camissonia*	2	10	12
VII. *Eremothera*	2	[e] 5	7
VIII. *Chylismiella*	–	1	1
IX. *Nematocaulis*	–	2	2
	17	44	61

[a] *C. confertiflora*, *C. eastwoodiae*, and *C. parryi* not tested but listed here provisionally.
[b] *C. tanacetifolia* seems to include self-compatible populations.
[c] Some populations of *C. subacaulis* might be self-incompatible.
[d] *C. cheiranthifolia* subsp. *suffruticosa* in part only; subsp. *cheiranthifolia* wholly self-compatible.
[e] *C. nevadensis* might be self-incompatible, but this seems unlikely.

Of the nine sections recognized in this revision, three small ones contain no self-incompatible species; one (*Chylismia*) consists mainly of self-incompatible species; and the other five contain one or two self-incompatible species each, with a majority of self-compatible ones. It is interesting that of the two groups associated with the most severe desert, *Chylismia* and *Eremothera*, the former is the only section in which as many as half of the species, including nearly all of the common ones, are self-incompatible, and the most widespread species of the latter, *Camissonia boothii*, is likewise self-incompatible. One normally associates exploitation of a desert habitat with self-compatibility or autogamy, but this has evidently not been the case here; perhaps the ability to adjust to the rapidly shifting desert habitats calls for a maximum of recombination, and this is precisely what seems to be favored in both groups, which conform to the definition of homogamic complexes (Raven, Univ. Calif. Publ. Bot. 34: 66–67. 1962).

If pinnately lobed or divided leaves are primitive for the genus *Camissonia*, as the evidence appears to indicate, there have been evolutionary trends toward simple leaves in sect. *Eulobus* (where some populations of *Camissonia crassifolia*, such as those on Isla de Cedros, have lobed leaves, while most others have entire leaves) and sect. *Chylismia* (where lobed or divided leaves predominate, although some species have lost them). Sect. *Lignothera* appears to be a derivative of sect. *Chylismia*, specialized for hawk-moth pollination in its long hypanthia, the longest in the genus. In the two species comprising this group, the pollen is shed in tetrads, a characteristic otherwise unknown in the tribe Onagreae. In sect. *Tetrapteron*, *Camissonia tanacetifolia* and

C. breviflora are characterized by deeply lobed leaves, as are some populations of *C. subacaulis;* whereas the remaining perennial species, *C. ovata,* has entire leaves, as do the two annuals. The superficial similarity between these two annual members of sect. *Tetrapteron* and some species of sect. *Holostigma* provides a clue as to the relationships of the latter group, but probably tells us nothing about the exact route of its derivation.

Within the last five groups listed here, relationships are almost entirely obscure. Sect. *Holostigma* includes the only perennial species and perhaps is morphologically the most generalized of the five sections. There does not, however, appear to be any evidence for close relationship between this group and any other. Sect. *Camissonia* consists entirely of yellow-flowered species, like sect. *Holostigma;* but no species are transitional between the two groups and there is no evidence for close relationship between them. Polyploidy is important in both of these sections, which have diversified largely in the areas derived from the Madro-Tertiary Geoflora and now center in California, with one group of sect. *Camissonia* (species 40–43) centering in the northern Great Basin. Sect. *Eremothera,* consisting of white-flowered species, does not exhibit any evident relationship to any other group, and it seems certain that white-flowered species evolved at least three times in the history of the genus, once here, once in *C. claviformis* (sect. *Chylismia*), and once in *C. pterosperma* (the only species of sect. *Chylismiella*). In the first two instances, the acquisition of white flowers was undoubtedly associated with a shift from bee-pollination to pollination by small moths.

Almost nothing can be said about the relationships of the last two small sections, *Chylismiella* (with one species) and *Nematocaulis* (with two very closely related ones). The white petals of the former, yellow at the base, are found elsewhere in the tribe only in the genus *Gayophytum;* the seeds of *Camissonia pterosperma,* the only species of this section, are unique in the family. Likewise, the flattened capsules of both species of sect. *Nematocaulis* are reminiscent of those of *Gayophytum humile* A. L. de Jussieu, probably the most generalized species of its small genus (Lewis & Szweykowski, Brittonia 16: 343–391. 1964). It appears possible that these two small, distinctive sections of *Camissonia* have been derived from the same evolutionary line that gave rise to *Gayophytum,* but nothing more can be said about their relationships at this time.

Pollination Systems

Most outcrossing species of *Camissonia* are pollinated by bees, and a number of these bees are oligolectic, gathering pollen from no other plants (Linsley, MacSwain, & Raven, Univ. Calif. Publ. Entom.

33: 1–98. 1964). One group of two species, sect. *Lignothera*, has shifted to opening in the evening, when the plants are pollinated by hawk moths; these species have yellow flowers. The outcrossing species of the entirely white-flowered sect. *Eremothera* and the white-flowered and afternoon opening yellow-flowered subspecies of *Camissonia claviformis* (sect. *Chylismia*) are predominantly pollinated by small moths after their opening in the late afternoon or early evening, but in both groups secondary associations with oligolectic bees in the late afternoon have also evolved (Linsley et al., op. cit.). Two species of sect. *Chylismia*, *Camissonia megalantha* and *C. heterochroma*, are unique in the genus in having purple flowers. In both, the flowers open near sunrise; the former species is pollinated by bees, and the latter is autogamous. Finally, *C. pterosperma* has white petals that are yellow at the base and flowers that open in the morning. This pattern of petal coloration is found elsewhere in the tribe only in *Gayophytum*, where pollination by flower-flies and small bees predominates (MacSwain, Raven, & Thorp, MS.); but *Camissonia pterosperma* is largely if not entirely autogamous.

One of the most interesting aspects of the pollination system in *Camissonia*, and indeed in the Onagraceae as a whole, is the common occurrence of pairs of species—one member large-flowered and outcrossing (and sometimes self-incompatible), the other small-flowered and self-pollinating (and often a polyploid or complex structural heterozygote, depending on the group). In *Camissonia*, many examples of such pairs are evident: *C. multijuga-C. walkeri* subsp. *tortilis* (sect. *Chylismia*); *C. tanacetifolia-C. breviflora* (sect. *Tetrapteron*); *C. bistorta-C. lewisii* (sect. *Holostigma*); *C. kernensis* subsp. *kernensis-C. pubens* (sec. *Camissonia*); *C. refracta-C. chamaenerioides* (sect. *Eremothera*); and *C. hilgardii-C. andina* (sect. *Nematocaulis*). Autogamy doubtless arises with a certain frequency throughout the range of normally outcrossing species, but if it is to spread and become characteristic of entire populations, it must do so because it provides for the duplication of a genotype that is highly successful in some area. This has obviously occurred time after time in the evolution of the genus *Camissonia*.

Chromosome Numbers and Behavior

The earlier reports of chromosome number listed by Lewis, Raven, Venkatesh, and Wedberg (Aliso 4: 73–76. 1958) and those of Gregory and Klein (Aliso 4: 505–521. 1960) are repeated in this paper. On the other hand, the numerous chromosome counts I reported earlier for taxa of sect. *Chylismia*, *Lignothera*, and *Chylismiella* (Raven, Univ. Calif. Publ. Bot. 34: 1–122. 1962) are not included in this revision, although a few more recent determinations of chromosome numbers for these groups are reported. The only other familiar reports of

chromosome number in *Camissonia* are six undocumented counts listed by Johansen (Proc. Nat. Acad. Sci. U.S. 15: 882–885. 1929; Amer. Journ. Bot. 16: 595–597. 1929), without citation of locality or voucher, and the single, probably erroneous count reported by Bell and discussed below. Johansen's counts are mentioned in the accounts of the taxa to which they refer.

Aneuploidy is almost unknown in *Camissonia* and rare in the tribe Onagreae. Only in *Clarkia* (with basic chromosome numbers of $x=5$ 6, 7, 8, and 9) does aneuploidy seem to be a regular feature of the evolutionary pattern which often accompanies speciation. In *Camissonia*, at least two populations of the South American tetraploid *C. dentata* have $n=13$ instead of the usual $n=14$; this appears to be the only documented instance of aneuploidy in the genus. In these populations, aneuploidy does not appear to have had any important bearing on speciation. Bell (Sida 2: 169. 1965) reported $n=6$ in *Camissonia claviformis* subsp. *peeblesii* ("*Oenothera clavaeformis* var. *aurantiaca*") from Maricopa County, Arizona (*Bell* 17558, NCU). In the drawings made from the original preparations, however, which Dr. Bell has kindly allowed me to examine, it appears that $n=7$ is as likely a count as $n=6$. All other individuals of this species that have been examined cytologically (a total of 411) have had $n=7$.

Although detailed information about chromosome number and behavior is given throughout the text of this paper and in the appendix, and summaries are given for each section, it seems worthwhile to summarize the chromosomal information available for *Camissonia* at this point, as follows:

	Individuals	*Populations*	*Species*	*Additional subspecies*	*Polyploid taxa*	
					wholly	*partly*
I. *Eulobus*	108	78	4			1
II. *Chylismia*	683	239	13	14		2
III. *Lignothera*	36	23	2	2		
IV. *Tetrapteron*	49	46	6	1	1	1
V. *Holostigma*	389	335	14	3	5	
VI. *Camissonia*	192	181	12	4	[a] 9	
VII. *Eremothera*	67	57	7	5		1
VIII. *Chylismiella*	1	1	1			
IX. *Nematocaulis*	11	11	2		1	
	1536	971	61	29	16	5

[a] Including two Chilean populations of *C. dentata* subsp. *dentata* with $n=13$.

As can be seen from the table, the chromosomal sampling of *Camissonia* has been extensive. Counts are available for at least one population representing each of the nine sections, and for every species and subspecies except the following: *Camissonia confertiflora*, *C. speculicola* subsp. *hesperia*, and *C. scapoidea* subsp. *macrocarpa*, and subsp. *utahensis* of sect. *Chylismia*, and *C. gouldii* of sect. *Ere-*

mothera. Thus 59 of the 61 species recognized here and 85 of the 90 taxa have been examined cytologically. It seems unlikely that the pattern will be modified in any substantial way by further chromosome counts.

The polyploid plants examined in sect. *Eremothera* and sect. *Tetrapteron*, as well as the polyploids of *Camissonia walkeri* (sect. *Chylismia*), are clearly cytologically autopolyploid, with rings of chromosomes forming regularly at meiotic metaphase I. The hexaploid in sect. *Tetrapteron* has almost certainly been derived directly from the tetraploid; these two races are regarded as subspecies of *C. tanacetifolia*. The single diploid plant of this species that has been examined may well have been derived directly from a tetraploid individual as discussed in detail following the taxonomic treatment of the species.

With one possible exception (see appendix) no rings of chromosomes have been observed in the polyploids of sect. *Holostigma* and sect. *Camissonia*, and polyploidy has played the most important role in these two groups in the course of evolution. The same is true of the polyploids of sect. *Nematocaulis*. Morphological and geographical relationships make it virtually certain that the tetraploid populations in *C. californica* (sect. *Eulobus*) and in *C. scapoidea* subsp. *scapoidea* (sect. *Chylismia*) have had an autotetraploid origin, even though they do not form rings of 4 chromosomes at meiotic metaphase I. In all of these groups the chromosomal homology of the diploid entities (see below) makes it clear that the formation of multivalents in polyploids is genetically controlled, and prevented even if the diploid genomes present in a polyploid are largely homologous. In the further interpretation of these data, it is instructive to consider the occurrence of translocation heterozygotes in naturally occurring diploid populations of these sections. It is important to stress the occurrence of such heterozygotes in outcrossing taxa, as rings of chromosomes tend to be eliminated relatively rapidly in the course of autogamous reproduction, except in the special case of balanced structural heterozygosity.

In sect. *Chylismia*, translocation heterozygotes comprised about 20 percent of the individuals examined (Raven, Univ. Calif. Publ. Bot. 34: 40. 1962), and the more limited amount of information available for sect. *Eremothera* suggests that a comparable level of heterozygosity may obtain here also. In one plant of *Camissonia refracta*, a member of this section, a ring of 10 chromosomes was found at diakinesis; this was the largest ring found in the genus. The situation in other well-sampled groups is, however, very different. In sect. *Camissonia*, only about 2 percent of the outcrossing individuals examined had a ring of chromosomes at meiotic metaphase; and in sect. *Holostigma*

and sect. *Eulobus*, no multivalents have been observed, even though approximately 500 plants of the two groups have been examined. Even if reciprocal translocations occur frequently in these sections, they must be eliminated rapidly from the populations.

One naturally associates the frequent occurrence of reciprocal translocations within the populations of a species with the role of such translocations in the differentiation of species in the same group. It might therefore be expected that patterns of chromosomal differentiation between species would be different in sect. *Chylismia* from those observed in sects. *Holostigma* and *Camissonia*. This does not, however, appear to be the case; interspecific hybrids in all three groups show chromosomal configurations which indicate that their parents differ by, usually, 2–4 reciprocal translocations. Thus the appearance of reciprocal translocation configurations at a high frequency within the populations of a species may have little to do with the patterns of differentiation between populations of the group. In all three sections, there is a high degree of chromosome association in diploid interspecific hybrids; hence, the control of multivalent formation in polyploids must have a genetic basis and not be related, for example, to the frequent formation of univalents in interspecific hybrids in some of the groups. It may be significant, however, that pair-forming polyploids are frequent and evolutionarily important in those sections in which reciprocal translocations are infrequent or rare in natural populations, and virtually absent in those groups in which reciprocal translocations are abundant in natural populations.

Finally, sect. *Chylismia* is the only group of the genus in which supernumerary chromosomes have been noted. Here, one or more supernumeraries were found in some 3.7 percent of the nearly 700 individuals examined (Raven, Univ. Calif. Publ. Bot. 34: 41. 1962), this observation according well with an earlier hypothesis of a causal relationship between translocation heterozygosity and supernumerary formation (Lewis, Evolution 5: 142–157. 1951; Lewis & Raven, Rec. Adv. Bot. 1466–1469. 1961). Supernumeraries might be expected to occur in sect. *Eremothera* if more extensive sampling was carried out.

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Wyoming (RM); Herbarium of the Komarov Botanical Institute of the Academy of Sciences of the U.S.S.R., Leningrad (LE); Intermountain Herbarium, Utah State Agricultural College (UTC); British Museum (Natural History), London (BM); University of California, Los Angeles (LA); Los Angeles County Museum (LAM); University of Wisconsin, Madison (WIS); Tulane University Herbarium, New Orleans (NO); The New York Botanical Garden (NY); University of Notre Dame (ND): National Museum of Canada, Ottawa (CAN); Plant Research Institute, Canada Department of Agriculture, Ottawa (DAO); University of Oxford (OXF); Muséum National d'Histoire Naturelle, Paris (P); Academy of Natural Sciences, Philadelphia (PH); Idaho State College Herbarium, Pocatello (IDS); Brigham Young University, Provo, Utah (BRY); Washington State University, Pullman (WS); University of Nevada, Reno (RENO); Nevada Agricultural Experimental Station, Reno; Missouri Botanical Garden, St. Louis (MO); Peck Herbarium of Willamette University, Salem, Oregon; University of Utah, Salt Lake City (UT); San Diego Museum of Natural History (SD); San Diego State College (here given as SDSC); California Academy of Sciences, San Francisco (CAS); California State Polytechnic College, San Luis Obispo (OBI); Santa Barbara Botanic Garden, Santa Barbara, California (SBSG); Santa Barbara Museum Of Natural History (SBM); University of California, Santa Barbara (UCSB); Museo Nacional de Historia Natural, Santiago, Chile (SGO); University of Washington, Seattle (WTU); Dudley Herbarium, Stanford University, Stanford, California (DS); New Mexico College of Agricultural and Mechanical Arts, State College (NMC); Naturhistoriska Riksmuseum, Stockholm (S); Desert Botanical Garden, Tempe, Arizona (DES); University of British Columbia, Vancouver, British Columbia (UBC); U.S. National Museum, Washington (US); U.S. National Arboretum, Washington (NA). In addition, I have examined the material of *Camissonia* in the private herbarium of Ernest C. Twisselmann, Cholame, California.

Systematic Treatment

Camissonia Link

Camissonia Link, Jahrb. Gewaechsk. 1: 186. 1818.

Sphaerostigma (Seringe) Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 49. 1835. Based on *Oenothera* sect. *Sphaerostigma* Seringe, *in* DC., Prod. 3: 46. 1828. Lectotype: *O. dentata* Cav.= *Camissonia dentata* (Cav.) Reiche.

Agassizia Spach, Hist. Veg. Phan. 4: 347. 1835; not Chavannes 1830. Type: *A. cheiranthifolia* (Hornem. ex Spreng.) Spach=*Camissonia cheiranthifolia* (Hornem. ex Spreng.) Raimann.

Holostigma Spach, Nouv. Ann. Mus. Paris III. 4: 332. 1835.

Eulobus Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 514. 1840. Type: *E. californicus* Nutt. ex Torr. & Gray = *Camissonia californica* (Nutt. ex Torr. & Gray) Raven.

Chylismia (Nutt. ex Torr. & Gray) Raimann, *in* Engl. & Prantl, Natürl. Pflanzenfam. III. 7: 217. 1893. Based on *Oenothera* subg. *Chylismia* Nutt. ex Torr. & Gray.[1] Type: *O. scapoidea* Torr. & Gray = *Camissonia scapoidea* (Torr. & Gray) Raven.

Taraxia (Nutt. ex Torr. & Gray) Raimann, *in* Engl. & Prantl, Natürl. Pflanzenfam. III. 7: 216. 1893. Based on *Oenothera* subg. *Taraxia* Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 506. 1840. Lectotype: *O. breviflora* Torr. & Gray = *Camissonia breviflora* (Torr. & Gray) Raven.

Annual or perennial herbs, rarely subshrubs, from a taproot which in some species branches and gives rise to new plants. Leaves basal or cauline and spirally arranged, largest near the base, reduced upward. Flowers opening near sunrise, or in a few taxa near sunset or in the late afternoon, the stigma receptive and anthers shedding pollen simultaneously and immediately and the flowers withering in less than a day, 4-merous or very rarely 3-merous. Petals yellow, rose-purple, or white, reflexed in anthesis in the outcrossing species. Stamens and style yellowish, the stigma greenish yellow. Stamens 8, the episepalous ones longer, or very rarely 4, the epipetalous ones lacking; anthers versatile or basifixed (in sect. *Tetrapteron*), the sporogenous tissue in each locule undivided. Pollen yellow, shed singly or (in sect. *Lignothera*) in tetrads. Stigma capitate or hemispherical. Capsule loculicidal, usually promptly so, straight or contorted, the seeds in 1 or 2 rows in each of the 4 locules, usually adhering to the central partition following dehiscence. Basic chromosome number, $x=7$. Self-incompatibility known in approximately 17 of the 61 species.

Type species: *Camissonia flava* Link = *C. dentata* (Cav.) Reiche.

In the following treatment, an effort has been made to group related species. Within each section, generalized species are listed first, more specialized ones later. The keys have been written for ease of identification and are not intended to display relationships. Sympatric entities have been listed within each section following the taxonomic treatment of each taxon. In the same place a summary of the available chromosomal information and that on self-incompatibility is presented. Only a digest of my earlier treatment of sects. *Chylismia*, *Lignothera*, and *Chylismiella* (Raven, Univ. Calif. Publ. Bot. 34: 1–122. 1962) is presented here, but I have tried to include enough information to make the present revision complete and usable taxonomically without reference to the earlier paper. In the citation of collections, R has consistently been used for *Raven*, except in the case of type collections. Voucher specimens are understood to be

[1] As to the status accorded this and comparable groups, see Brizicky, Journ. Arn. Arb. 44: fn. 1963, and Gray, Man. Bot. N. U.S., ed. 2, p. xi., 1856.

deposited in the Dudley Herbarium, Stanford University (DS), with duplicates in the U.S. National Museum (US) and Rancho Santa Ana Botanic Garden, Claremont, California (RSA), in most cases, unless some other indication of their deposition is made.

Key to Sections

Ovary with a long slender sterile projection below the hypanthium, the plants acaulescent or nearly so . . . . . Section IV. **Tetrapteron**

Ovary lacking a sterile projection, the plants only occasionally appearing acaulescent, and then when immature.

Seeds with a thick papillate wing surrounding the concave face (fig. 78); petals white, yellow near the base . . . . . Section VIII. **Chylismiella**

Seeds not winged; petals yellow, white, or purple.

Capsules on well-defined pedicels, not coiled or contorted; seeds in 2 rows in each locule.

Hypanthium 0.4–8 mm. long; leaves basal or cauline, often pinnately divided or lobed; pollen shed singly . . . . . Section II. **Chylismia**

Hypanthium 4.5–40 mm. long; leaves all cauline, simple, usually cordate-orbicular; pollen shed in tetrads . . . . . Section III. **Lignothera**

Capsules sessile (see also 40. *C. kernensis*), often coiled or contorted; seeds in 1 row in each locule.

Petals white, the flowers vespertine . . . Section VII. **Eremothera**

Petals yellow, the flowers matinal.

Leaves pinnately lobed, more rarely subentire; petals usually with a pattern of minute maroon flecks near the base; seeds often with purple dots or blotches; capsules often sharply reflexed at maturity (Baja California, Sonora, southern California, Arizona).

Section I. **Eulobus**

Leaves subentire; petals unspotted or with 1 or 2 bright red spots near the base; seeds unspotted; capsules not reflexed (widespread).

Plants with naked, capillary stems, each bearing a crowded, leafy inflorescence at its apex; capsule strongly flattened, 0.5–1 cm. long . . . . . Section IX. **Nematocaulis**

Plants usually leafy from the base, the inflorescence not crowded; capsule not flattened, usually over 1 cm. long.

Capsules quadrangular, at least when dry; plants usually with flowers at the basal nodes; leaves mostly lanceolate to ovate; seeds dull, flattened, usually over 1 mm. long.

Section V. **Holostigma**

Capsules subterete; plants lacking flowers at the basal nodes; leaves mostly linear or very narrowly elliptic; seeds shining, triangular in transection, often under 1 mm. long.

Section VI. **Camissonia**

SECTION I. EULOBUS

Stigma cylindrical, 1.4–4.5 mm. long; branches prostrate, radiating from a central axis (central and southern Baja California) . . . . . **3. C. sceptrostigma**

Stigma globose; branches erect.

Woody perennials, often flowering the first year; stigma held well above the anthers at anthesis; leaves usually entire (west coast of Baja California). **1. C. crassifolia**

Annuals; stigma equaled by at least the longer stamens, their anthers surrounding it at anthesis; leaves usually deeply pinnatifid.
Capsules usually more or less contorted; hypanthium 3–4.2 mm. long; petals 10–19 mm. long (central Baja California) . . . . . **2. C. angelorum**
Capsules straight or nearly so, deflexed at maturity; hypanthium 0.6–1.5 mm. long; petals 6–14 mm. long (widespread) . . . . **4. C. californica**

SECTION II. CHYLISMIA

Stamens 4 (local in Mohave and Coconino Cos., Arizona) . . . . . **15. C. exilis**
Stamens 8.
Corollas lavender in anthesis.
Stigma held above anthers at maturity; hypanthium 4.5–8.5 mm. long; petals 9–13.8 mm. long . . . . . **16. C. megalantha**
Stigma surrounded by anthers at maturity; hypanthium 2–5 mm. long; petals 2–6 mm. long . . . . . **17. C. heterochroma**
Corollas yellow or white at anthesis.
Capsules distinctly clavate, more than 2 mm. thick (see also 9. *C. walkeri*). Stigma surrounded by anthers at maturity, the petals less than 5.5 mm. long.
Oil cells lining veins on underside of leaves pale yellowish brown, rarely darker; leaves often simple and entire, in compact basal rosette.
Capsules to 30 mm. long; leaf blades to 5.5 cm. long; base of plants often nearly glabrous (Wyoming, Colorado, eastern Utah, New Mexico) . . . . . **13a. C. scapoidea** subsp. **scapoidea**
Capsules 25–40 mm. long; leaf blades to 3.5 cm. long; base of plants densely strigose (Arizona) . **13b. C. scapoidea** subsp. **macrocarpa**
Oil cells lining veins on underside of leaves dark brown, conspicuous; leaves remotely dentate and often pinnately compound, in loose basal rosette.
Leaves with several palrs of lateral leaflets; capsules 16–38 mm. long; petals 4–8 mm. long (western Utah and adjacent Neveda). **13d. C. scapoidea** subsp. **utahensis**
Leaves with lateral leaflets few or absent; capsules rarely over 20 mm. long; petals 1.8–4 mm. long (Oregon, Idaho, western Utah, and Nevada) . . . . . **13c. C. scapoidea** subsp. **brachycarpa**
Stigma held well above anthers at maturity, the petals usually more than 6 mm. long.
Mature pedicels and capsules sharply deflexed; corollas bright yellow. **11. C. munzii**
Mature pedicels and capsules ascending or spreading; corollas yellow or white.
Branches of the inflorescence numerous and filiform; leaves not strictly basal; capsules less than 10 mm. long, the pedicels slender (southwestern Utah and northwestern Arizona) . . **14. C. parryi**
Branches of inflorescence not filiform; leaves mostly in a basal rosette; capsules often more than 10 mm. long.
Stamens differentiated into 2 sets; inflorescence loose; leaves entire or nearly so, rounded, often simple and glabrous (Colorado and Utah) . . . . . **12. C. eastwoodiae**
Stamens subequal; inflorescence dense; leaves generally dentate, often acutely angled, pinnate and pubescent (Oregon and Nevada southward).

Lower parts of the plants with villous, spreading pubescence; sepals with free caudate projections arising below apices.
Petals fading reddish (Arizona, Sonora, Baja California).
Petals 3–5 mm. long; style 7–12 mm. long (Arizona, and Sonora) . . . . . **10k. C. claviformis** subsp. **rubescens**
Petals 1.5–2 mm. long; style 5–7 mm. long (Baja California) **10j. C. claviformis** subsp. **wigginsii**
Petals not fading reddish (San Diego and Imperial Cos., California, and adjacent Baja California) **10h. C. claviformis** subsp. **peirsonii**
Lower parts of plants short-appressed pubescent or glabrous but not villous with spreading trichomes; sepals entire or with caudate projections.
Petals white, the hypanthium orange brown.
Plants variously pubescent on stems and in inflorescence; lateral leaflets often reduced.
Lateral leaflets reduced in number, the leaves often nearly simple; basal rosette compact (Nevada, southern Oregon, local in Mono and Inyo Cos., California). **10c. C. claviformis** subsp. **integrior**
Lateral leaflets generally well developed and numerous, the basal rosette not compact.
Sepals often with projections arising below the apices; terminal leaflets often large and nearly cordate; buds and inflorescences often silky-strigose (Death Valley region, California). **10d. C. claviformis** subsp. **funerea**
Sepals usually entire; terminal leaflets usually inconspicuous; buds and leaflets not silvery.
Pubescence on leaves, stems, and often inflorescences glandular (Arizona). **10g. C. claviformis** subsp. **peeblesii**
Pubescence on leaves and stems rarely glandular, that of inflorescences never so (southern Nevada, California, rare in Arizona). **10f. C. claviformis** subsp. **aurantiaca**
Buds and inflorescences usually glabrous or nearly so; lateral leaflets usually well developed (western deserts of California) . . **10e. C. claviformis** subsp. **claviformis**
Petals yellow, the hypanthium yellow or orange brown.
Plants with strigose pubescence above and in the inflorescence, the sepals sometimes with free projections (southern California, Arizona, and northern Mexico). **10i. C. claviformis** subsp. **yumae**
Plants usually glabrous above, the sepals entire; northern part of species range.
Leaves lanceolate, narrow, and evenly dentate, often nearly entire by loss of lateral leaflets; hypanthium dark (Inyo and Mono Cos., California). **10b. C. claviformis** subsp. **lancifolia**
Leaves pinnate, the terminal leaflets ovate, often blunt, the lateral leaflets often well developed (Washoe Co., Nevada, northward). **10a. C. claviformis** subsp. **cruciformis**

Capsules elongate, often linear, usually less than 2 mm. thick; pedicels often inconspicuous.
Stigma surrounded by anthers at maturity; petals less than 6 mm. long; style less than 6 mm. long; inflorescence erect in bud.
Clumped perennials with somewhat woody base; leaves glabrous or sparsely pubescent; anthers glabrous (Colorado R. in and below Grand Canyon, Arizona).
Leaves and style glabrous . . . **8a. C. speculicola** subsp. **speculicola**
Leaves and style pubescent . . . **8b. C. speculicola** subsp. **hesperia**
Annuals or short-lived perennials, the base usually not at all woody; leaves pubescent, usually densely so; anthers pubescent or glabrous (widespread) . . . . . **9. C. walkeri**
Stigma elevated above anthers at maturity; petals usually more than 6 mm. long; style more than 6 mm. long.
Inflorescence erect or drooping, elongating before flowers open, the mature buds mostly individually pendulous; plants virgate; hypanthium less than 3 mm. long (Utah, southern Nevada, and northwestern Arizona). **7. C. multijuga**
Inflorescence drooping, mostly elongating after flowers open; stems stout, not virgate; hypanthium more than 3 mm. long.
Sepals with free caudate tips arising just below apices, glandular-pubescent; inflorescence often branched; stamens differentiated into 2 sets (Toroweap area, Mohave Co., Arizona). **5. C. confertiflora**
Sepals lacking free caudate tips, or if they are present, the sepals variously pubescent, but not glandular; inflorescence branched or unbranched; stamens subequal (widespread) . **6. C. brevipes**

SECTION III. LIGNOTHERA

Hypanthium 18–40 mm. long; style 30–58 mm. long . . . . **19. C. arenaria**
Hypanthium 4.5–14 mm. long; style 8–23 mm. long.
Leaves ovate-acuminate, longer than broad; petals less than 4.5 mm. long; pubescence predominantly glandular. **18. C. cardiophylla** subsp. **cedrosensis**
Leaves cordate to cordate-orbicular, about as long as broad; petals mostly more than 4.5 mm. long.
Plants coarse; pubescence mostly glandular (Inyo Co., California). **18b. C. cardiophylla** subsp. **robusta**
Plants more slender; pubescence mostly villous (San Bernardino Co., California, southward and eastward). **18a. C. cardiophylla** subsp. **cardiophylla**

SECTION IV. TETRAPTERON

Plants perennial, strictly acaulescent; capsule not winged.
Leaves pinnatifid, the plants more or less densely pilose or appressed pubescent.
Style 9.5–20 (–25) mm. long, the stigma held above the anthers at anthesis; petals (8–) 10–23 mm. long.
Less than 5 percent of pollen 4-pored; pubescence variable (widespread). **22a. C. tanacetifolia** subsp. **tanacetifolia**
More than 10 percent of pollen 4-pored; plants densely gray-pubescent (Sierra Valley area in Plumas and immediately adjacent Lassen and Sierra Cos., California) . **22b. C. tanacetifolia** subsp. **quadriperforata**
Style 3–6.5 mm. long, the stigma surrounded by anthers of longer stamens at anthesis; petals 5.5–7 (–8) mm. long . . . . . **23. C. breviflora**

Leaves not pinnatifid or, if so, plants subglabrous.
Leaves more or less densely white-ciliate; capsule subterete, the thin walls much distended by the seeds . . . . . **20. C. ovata**
Leaves subglabrous, rarely minutely and sparsely strigulose; capsule more or less 4-angled, the nearly flat walls not distended by the seeds.
21. C. subacaulis

Plants annual, sometimes branching; capsule broadly winged in upper half.
Petals 5–18 mm. long; style 3–5.5 mm. long; pubescence pilose.
24. C. graciliflora
Petals 2–3.5 mm. long; style 1–2.2 mm. long; pubescence strigose . **25. C. palmeri**

SECTION V. HOLOSTIGMA

Plants perennial, often somewhat woody near the base.
Petals (10–)12–20 mm. long; styles 13–23 mm. long (near Goleta, Santa Barbara Co., California, south to near San Quintín, Baja California; San Nicolas and San Martin Isls.) . . . **26a. C. cheiranthifolia** subsp. **suffruticosa**
Petals 6–11 mm. long; styles 6–9 mm. long (Point Conception, Santa Barbara Co., California, north to Coos Bay, Curry Co., Oregon; several islands).
26b. C. cheiranthifolia subsp. **cheiranthifolia**

Plants annual (except for a few populations of *C. bistorta*, q.v.).
Stigma evidently held above the anthers at anthesis, the flowers large (southern California, north to Ventura Co., and adjacent Baja California).
27. C. bistorta
Stigma surrounded by at least the anthers of the longer set of stamens at anthesis, the flowers small to large (widespread).
Capsule very heavy, 2.8–3.5 mm. thick near the base, straight or nearly so, deeply grooved along the lines of dehiscence (Guadalupe and San Clemente Isls.).
Pubescence strigose; petals not spotted (Guadalupe Isl.).
28a. C. guadalupensis subsp. **guadalupensis**
Pubescence spreading; petals with a prominent red dot near the base (San Clemente Isl.) . . . **28b. C. guadalupensis** subsp. **clementina**
Capsule 0.75–2.2 mm. thick near the base, straight or curved into 1 or more spirals, not deeply grooved (widespread).
Pollen 25–100 percent 4- or 5-pored; hexaploid species.
Inflorescence lacking glandular trichomes; 4-pored pollen comprising 25–60 percent of the total (Santa Lucia Mts., Monterey Co., and inner Coast Ranges south to Santa Barbara Co., California).
38. C. luciae
Inflorescence with an understory of short glandular trichomes; 4- and 5-pored pollen comprising 70–100 percent of the total (not in area of *C. luciae*).
Capsule 1.3–1.6 mm. thick, subterete in transection (southernmost Monterey to central San Luis Obispo Co., California).
37. C. hardhamiae
Capsule 1.5–2 mm. thick, more or less quadrangular in transection (San Diego Co., California, and adjacent Baja California; offshore islands) . . . . . **39. C. robusta**
Pollen up to 5 percent 4-pored (rarely more in *C. intermedia*); diploid or tetraploid species.
Capsule markedly quadrangular in transection, 1.8–2.2 mm. thick (Los Angeles Co., California, south throughout the northwestern quarter of Baja California) . . . . . **29. C. lewisii**

Capsule not markedly quadrangular in transection, at least in living material, 0.75–1.2 (–1.8) mm. thick (widespread).
Plants subglabrous, usually with 50 or more flowers in the basal rosette, subcaespitose or with very thick prostrate branches from the base (coastal Baja California) . . . . . **30. C. proavita**
Plants subglabrous to densely villous, with few flowers in basal rosette (widespread).
Upper leaves evidently petiolate, attenuate at the base; capsule usually more contorted; plants subglabrous to strigulose, often reddish (Yolo Co., California, to 30° N. lat. in Baja California; Madera Co., California; Santa Cruz Isl.) . . . **33. C. ignota**
Upper leaves usually not evidently petiolate, rounded or truncate at the base; capsule straight to coiled once or twice; plants strigulose to villous, always evidently so (widespread).
Conspicuously gray-strigose plants of the deserts, the branches usually decumbent (deserts of southern California to Arizona and northern Baja California).
Petals 6.5–13 mm. long; style 6.5–10.5 mm. long (western Riverside and San Bernardino Cos., California).
34a. C. pallida subsp. **hallii**
Petals (2–) 3.5–6 (–8) mm. long; style (2.1–) 3–6.5 mm. long (widespread on deserts) . . **34b. C. pallida** subsp. **pallida**
Plants not conspicuously gray-strigose, barely reaching the margins of the deserts (except for *C. confusa* in central Arizona).
Capsule 0.75–0.9 mm. thick; upper leaves narrowly ovate or ovate; plants erect; $n=7$ . . . . . **32. C. hirtella**
Capsule 0.9–1.2 (–1.8) mm. thick; upper leaves narrowly lanceolate to narrowly ovate; plants erect or decumbent; $n=7$ or 14.
Plants with decumbent branches from the basal rosette; upper leaves usually narrowly lanceolate; short glandular trichomes usually absent in inflorescence; $n=7$ (Coast Ranges of California, Sonoma Co. to San Diego Co.) . . . . . **31. C. micrantha**
Plants erect; upper leaves lanceolate or narrowly ovate; short glandular trichomes almost always present in inflorescence; $n=14$ (widespread).
Plants gray-villous; petals (2.5–) 5–10.5 mm. long; style (2.5–) 4.5–7.5 mm. long (San Luis Obispo Co. to San Diego Co., California; central Arizona).
36. C. confusa
Plants usually not gray-villous; petals 1.5–3.5 (–4.5) mm. long; style 2–3.5 mm. long (Lake and Yolo Cos., California, to 30° N. lat. in Baja California; Santa Cruz and Santa Catalina Isls.) . . **35. C. intermedia**

SECTION VI. CAMISSONIA

Plants of North America.
Sepals reflexed singly; plants often with conspicuous spreading pubescence (Great Basin and neighboring areas).
Stigma elevated well above the anthers at anthesis; petals 8–15 (–18) mm. long.

Plants compact, the leaves clustered at the base; pubescence dense, spreading; fruiting pedicel 3–15 mm. long (northeastern Kern Co., California) . . . . . **40a. C. kernensis** subsp. **kernensis**

Plants not compact, the leaves not clustered at the base; pubescence variable; fruiting pedicel 0–5 (–15) mm. long (Kern, Inyo, Mono, and San Bernardino Cos., California, and adjacent Neveda).

40b. C. kernensis subsp. **gilmanii**

Stigma surrounded by the anthers at anthesis; petals 1.8–4 mm. long.

Basal rosette well developed, the plants usually with long, spreading trichomes.

Leaves 0.4–1.8 mm. wide; hypanthium 0.8–1.6 mm. long; style 1.6–3.2 mm. long; $n=7$ . . . . . **41. C. pusilla**

Leaves 2–5 (–6.2) mm. wide; hypanthium 1.3–3 mm. long; style 3.2–4.1 mm. long; $n=14$ . . . . . **42. C. pubens**

Basal rosette not well developed, the stems bare near the base; plants usually with appressed pubescence or subglabrous . . **43. C. parvula**

Sepals usually reflexed in pairs, remaining attached (widespread).

Stigma held above the anthers at anthesis; petals (3.5–) 4–15.5 mm. long.

Leaves lanceolate or narrowly ovate, entire or nearly so (Sierra Nevada, California, in Madera and Mariposa Cos.)

45a. C. sierrae subsp. **sierrae**

Leaves linear to narrowly elliptic or narrowly oblanceolate, serrulate to coarsely serrate (widespread in California).

Leaves linear to narrowly elliptic or narrowly oblanceolate, serrulate or serrate; stems usually erect (widespread in central and southern California). . . . . **44a. C. campestris** subsp. **campestris**

Leaves narrowly elliptic, coarsely serrate; plants usually decumbent (southern Monterey to northern Santa Barbara Co., California).

44b. C. campestris subsp. **obispoensis**

Stigma surrounded by the anthers at anthesis.

Leaves entire, very rarely with 1 or 2 small teeth; pubescence dense, strigulose (upper Kern R. drainage, California) . . **50. C. integrifolia**

Leaves serrulate or serrate; pubescence variable (widespread).

Leaves narrowly elliptic, rounded or obtuse at the base; $n=7$ (central Sierra Nevada, California).

Petals 4–7 mm. long; style 4.5–7 mm. (Madera and Mariposa Cos., California) . . . . . **45a. C. sierrae** subsp. **sierrae**

Petals 2.2–4 mm. long; style 2.8–5 mm. long (Fresno Co., California).

45b. C. sierrae subsp. **alticola**

Leaves linear or very narrowly elliptic, narrowly cuneate or attenuate at the base; $n=14$, 21 (widespread).

Often more than 30 percent of the pollen grains 4-pored; plants usually with spreading pubescence on the stems; $n=21$ (widespread in California south to Kern Co.) . . . . . **51. C. contorta**

Very rarely with more than 10 percent of the pollen grains 4-pored; pubescence variable; $n=14$ (California from Lake Co. southward, and adjacent Baja California).

Petals (4–)4.5–7 mm. long; style 4–7 mm. long; pubescence of stems long, spreading (Lake Co. and Sierra Nevada foothills from Eldorado Co. to Fresno Co., California). . . **46. C. lacustris**

Petals 2.1–4.2(–4.5) mm. long; style 2.3–4.8 mm. long; pubescence variable (Coast Ranges from Sonoma Co., California, south to northern Baja California, and Sierra Nevada of Kern Co., California).

Plants villous, the inflorescence glandular (serpentine soils, San Benito Co., California) . . . . . **47. C. benitensis**

Plants strigulose or with villous trichomes on the lower stem, rarely villous and glandular only (widespread in range given above). **48. C. strigulosa**

Plants of South America.

Leaves linear or very narrowly lanceolate; plants erect, decumbent, or prostrate; capsules 0.6–0.9 mm. thick (widespread) . . **49a. C. dentata** subsp. **dentata**

Leaves broadly elliptical, thick; plants prostrate; capsules 1.1–1.3 mm. thick, heavy (coastal sands in Prov. Concepción, Arauco, and Cautín, Chile). **49b. C. dentata** subsp. **littoralis**

SECTION VII. EREMOTHERA

Capsules not thickened near the base; plants lacking flowers at the lower nodes.

Petals 3.5–7 mm. long; stigma held well above the anthers at anthesis. **52. C. refracta**

Petals 1.8–3 mm. long; stigma surrounded by the anthers at anthesis. **53. C. chamaenerioides**

Capsules thickened near the base; plants with or without flowers at the lower nodes.

Inflorescence erect to the tip at anthesis; plants flowering from the base.

Petals 3–5 mm. long; style 6–7 mm. long, glabrous (west-central Nevada). **57. C. nevadensis**

Petals 0.8–1.3 mm. long; style 1.2–3.2 mm. long, pubescent near the base (widespread) . . . . . **58. C. minor**

Inflorescence nodding at anthesis; plants flowering from near the base or not.

Petals (3–) 4–7.5 mm. long; stigma held well above the anthers at anthesis.

Cluster of large basal leaves prominent at the time of flowering, the inflorescence relatively leafless; plants blooming in the spring, never with prominent spreading pubescence.

Capsules 2–3.8 mm. thick near the base, woody, the inflorescence very condensed (Sonoran and eastern Mojave Desert; San Juan Co., Utah) . . . . . **54c. C. boothii** subsp. **condensata**

Capsules 1–2.3 mm. thick near the base, not woody, the inflorescence not highly condensed.

Capsules 1.7–2.3 mm. thick near the base, curved outward (cismontane central and southern California, south to Los Angeles Co.). **54a. C. boothii** subsp. **decorticans**

Capsules 1–1.6 mm. thick near the base, often curved downward (western Mojave Desert of California; upper Kern R. drainage). **54b. C. boothii** subsp. **desertorum**

Cluster of basal leaves rarely prominent at time of flowering, the inflorescence leafy; plants blooming in summer or late spring, often with prominent spreading pubescence.

Plants villous and glandular pubescent, blooming in the summer.

Plants usually 1.5–4 dm. tall, robust; cauline leaves coarsely serrulate, lanceolate or narrowly ovate (Mono Co., California, north to eastern Washington and southwestern Idaho; Mohave Co., Arizona) . . . . . **54f. C. boothii** subsp. **boothii**

Plants usually 0.5–2 dm. tall; cauline leaves serrulate, narrowly lanceolate or lanceolate (southern Lander and eastern Churchill Cos., Nevada, south to northeastern Inyo Co., California, and southern Nye Co., Nevada; Kingston Range, San Bernardino Co., California) . . . . . **54e. C. boothii** subsp. **intermedia**

Plants strigose, sometimes densely so, rarely villous or with an admixture of glandular trichomes; plants blooming in late spring and early summer (eastern Oregon and southern Idaho south to Lassen Co., California, through eastern Nevada to northern Clark Co., and in western Utah) . . . . . **54d. C. boothii** subsp. **alyssoides**

Petals 1.5–2.5 mm. long; stigma surrounded by the anthers at anthesis.

Pubescence villous and glandular; seeds dimorphic, the basal ones coarsely papillose (eastern Washington, eastern Oregon, southern Idaho). **55. C. pygmaea**

Pubescence glandular; seeds monomorphic, all smooth or nearly so (southwestern Utah and Coconino Co., Arizona) . . . . . **56. C. gouldii**

SECTION VIII. CHYLISMIELLA

One species . . . . . **59. C. pterosperma**

SECTION IX. NEMATOCAULIS

Petals 2.5–5 mm. long; style 4.5–6 mm. long (eastern Washington and along the Columbia R.) . . . . . **60. C. hilgardii**

Petals 0.8–2.3 mm. long; style 1.7–3 mm. long (widespread) . . . **61. C. andina**

Section I. *Eulobus*

Camissonia sect. *Eulobus* (Nutt. ex Torr. & Gray) Raven, Brittonia 16: 283. 1964.

Eulobus Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 514. 1840.

Oenothera sect. *Eulobus* (Nutt. ex Torr. & Gray) Baill., Hist. Pl. 6: 461. 1877.

Oenothera subg. *Eulobus* (Nutt. ex Torr. & Gray) Munz, Amer. Journ. Bot. 16: 254. 1929.

Woody subshrubs or annuals, the plants caulescent, flowering from near the base or not. Inflorescence erect. Flowers opening near sunrise. Ovary lacking a sterile projection. Hypanthium lined with a lobed, red brown, fleshy disc within or with a smaller, circular disc at the base of the style. Sepals reflexed separately or united. Petals yellow, usually finely flecked with red near the base, this area of the petals not ultraviolet reflective, the remainder of the petals strongly so; petals fading orange red after pollination. Stamens 8, subequal or with the epipetalous ones shorter; anthers versatile, villous or glabrous. Pollen shed singly. Capsule sessile, regularly and promptly loculicidal, the midrib of each valve yellowish brown, prominent, straight or contorted, somewhat torulose, subterete in living material, the seeds in 1 row in each locule. Seeds monomorphic, narrowly obovoid, more or less triangular in transection, pointing up or down in capsule, finely papillose.

Type species: *Camissonia californica* (Nutt. ex Torr. & Gray) Raven.

Distribution: Sandy slopes and flats, from southern San Benito, central Kern, and eastern San Bernardino Counties, California, and western and southern Arizona (from the vicinity of Kingman south),

south-central Sonora at about 28°20′ N. lat., and in Baja California to the vicinity of Bahía de la Magdalena at about 24°30′ N.; Santa Cruz and Santa Catalina Islands, California; Isla de Cedros, Baja California; and Isla San Lorenzo, Golfo de California.

Camissonia sect. *Eulobus* is here taken in exactly the same sense in which it was constituted by Munz in 1929 (Amer. Journ. Bot. 16: 253–257). At the time he prepared this revision, Dr. Munz remarked that herbarium material of three of the four species of this group was meager. In spite of this, the examination of the abundant material that has been collected in the succeeding 40 years has not given me any reason to disagree with the delimitation of species presented in 1929. I have, however, cited specimens to document the ranges of the three species endemic to Baja California, as this has not been possible until recently.

The woody *Camissonia crassifolia* appears to be the most generalized species within the group. It is one of the two self-incompatible species in the section and the only one known to be regularly associated with a group of oligolectic bees, one of which is *Andrena* (*Onagrandrena*) *eulobi* Linsley & MacSwain. *Camissonia angelorum* is closely related to and doubtless best thought of as an annual, self-pollinated derivative of *C. crassifolia*. More distantly related, but evidently derivable from the same ancestral stock, are the self-incompatible *C. sceptrostigma*, with its unique cylindrical stigma, of a form unknown elsewhere in Onagreae and the regularly self-pollinating *C. californica*, the most widespread species of the section and the only one to contain tetraploid populations. *Camissonia californica*, probably the most specialized species in the section, is rarely visited by insects.

In sect. *Eulobus*, 108 individuals have been examined chromosomally, representing 78 populations. Not one of these has had a multivalent association of chromosomes in meiosis, all being strictly pair-forming. In this respect, sect. *Eulobus* resembles sect. *Holostigma:* reciprocal translocations appear to play no adaptive role in natural populations, and multivalents have not been observed either in diploid or in polyploid populations, even though it is highly probable that some of the polyploids combine relatively homologous diploid genomes (see Appendix A, p. 381).

1. Camissonia crassifolia (Greene) Raven, Brittonia 16: 283. 1964.

Oenothera crassifolia Greene, Bull. Calif. Acad. 1: 188. 1885.

Erect well-branched shrub up to 1.4 m. tall, or sometimes prostrate; plants flowering the first year, and then as little as 1.5 cm. tall, with no distinct basal rosette, sometimes flowering at the basal nodes; plants subglabrous or with a few strigulose trichomes in the inflorescence, especially around the hypanthium and on the upper portions of the ovary. Leaves somewhat fleshy and glaucescent, narrowly

elliptic to narrowly lanceolate, rarely very narrowly elliptic, 1–6 cm. long, 2.5–12 mm. wide, entire to rather coarsely serrate or crenate, the apex obtuse, the base cuneate; leaves subsessile or with a petiole 1–2 mm. long. Inflorescence long and virgate. Hypanthium 1.5–2.5 mm. long, 2–3 mm. across at the summit, densely villous within. Sepals 5–9 mm. long, 1.2–2 mm. wide, reflexed in pairs or groups of 3 or 4. Petals (5.5–) 7.5–15 mm. long, (4–) 6.5–13 mm. wide, finely flecked with red in the basal third. Filaments of the episepalous stamens 3–7 mm. long, those of the epipetalous ones 2–5 mm. long; anthers 2.5–4 mm. long, sparsely long-ciliate or glabrous. Style (7–) 8.5–12 mm. long, densely villous in basal half; stigma globose, 0.8–1.1 mm. thick, held well above the stamens at anthesis. Capsules irregularly contorted, ca. 1.5–3.5 cm. long, 1.2–2 mm. thick. Seeds 1.7–2 mm. long, 0.7–0.8 mm. thick, brownish with small purple dots, often distorted or curved by the tough capsule walls. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: Cabo San Quintín, Baja California, 10 May 1885, *E. L. Greene* (ND; isotypes, BM, CAS, DS, F, GH, K, NY, US).

DISTRIBUTION (Figure 4): Sandy soil, especially on beaches, or rocky headlands, along the west coast of Baja California from just north of San Isidro, at about 31°20′ N. lat., to the region of Bahía de la Magdalena, at about 24°40′ N. lat.; ranging away from the immediate coast only in the region of the Desierto Vizcaíño at about 27° N. lat. Also on Isla de Cedros and Isla Santa Magdalena. From near sea level to a few hundred feet in elevation.

Vouchers for chromosome number (5 individuals, 5 populations), $n=7$:

BAJA CALIFORNIA: 3 mi. N. of San Quintín, *Breedlove* 4173 (progeny); 20.6 mi. S. of road to San Quintín, R12391 (K, LA, UC); Pabellon Beach, ca. 10 mi. S. of San Quintín, *Klein et al.* 13 (RSA, UC); Punta Baja, *Klein & Gregory* 1236; Isla Cedros, *Moran* 10763.

REPRESENTATIVE SPECIMENS EXAMINED:

BAJA CALIFORNIA: About 5 mi. N. of San Isidro, *Tillett* 799 (RSA); San Antonio del Mar (Johnson Ranch), *Chambers* 704 (DS, UC); Santo Domingo (Hamilton Ranch), *Nelson & Goldman* 7174 (US); W. of Bahía de San Quintín, *Wiggins* 11890 (DAO, DS, OSC, SD, UC); 14 mi. S. of San Quintín, *Raven* 17024 (RM, RSA, UC); Punta Baja, *Harbison* in 1950 (SD); Santa Catarina Landing, *Wiggins* 4438 (DS, GH, POM, US); ca. 14 mi. S. of Puerto San José, *Wiggins & Thomas* 207 (DS): Playa María, *Street* in 1875 (GH); 28 mi. SW. of Punta Prieta, *Haines & Stewart* in 1935 (ARIZ, DS, GH, K, LA, NY); Lagoon Head, 1889, *Palmer* 769 (GH, K, US); Viscaíño Depression S. and W. of Laguna Scammon, *Gentry* 7353 (ARIZ, DS, RSA, UC); Picachos de Santa Clara, *Gentry* 7740 (ARIZ, DS, UC); stabilized dunes 13 mi. W. of Rancho San Angel, *Wiggins* 16267 (DS); 1.6 km. E. of Laguna de San Ignacio, 59 km. SW. of San Ignacio, *Carter et al.* 2515 (DS); Punta Santo Domingo, *Nelson & Goldman* 7174 (POM); San Juanico, *Street* in 1876 (GH). CEDROS ISLAND: Slope above low beach cliffs, southwest coast, NNW. of Cerro Redondo, *Moran* 10772 (DS, SD); behind

beach NNW. of Cerro Redondo, *Moran* 10763 (DS, SD); W. coast 0.5–1 mi. NE. of Red Rock, *Haines & Hale* in 1939 (ARIZ, CAS, COLO, DS, POM, SD, UC). Isla Santa Magdalena: *Barclay* 3126 (BM, RSA), *Orcutt* 28 (GH, US). Mangrove I., Bahía de la Magdalena, *Greene* in 1938 (SD).

Colonies of *Camissonia crassifolia* may be variable in the degree of lobing of the leaves; thus *Gregory* 352 (RSA), from Pabellon Beach, has coarsely serrate leaves and *Gregory* 350 (RSA), which grew with it, has entire leaves. Collections with deeply lobed leaves are rather common, those of Palmer and Street cited above being extreme in this respect. Plants growing on the beach at certain localities are prostrate and distinctive in appearance. *Camissonia crassifolia* grows sympatrically with tetraploid populations of *C. californica*.

Plants from Isla de Cedros, where the species is local, flower regularly the first year. The flowers are borne in the rather compact rosette of deeply lobed leaves, and the plants only occasionally persist to flower a second year. A progeny of *Moran* 10763, from Isla de Cedros, and one from *Breedlove* 4173, from near San Quintín, on the mainland, were grown at Stanford, and both were found to consist entirely of self-incompatible plants. Reciprocal hybrids were made between these two strains and grown to maturity. In the F_1 individuals, the stems elongated rapidly and no flowers were formed at the basal nodes; in both of these respects they resembled the mainland parent. The F_1 individuals were self-incompatible like their parents and had 86 percent stainable pollen (based on a sample of 200 grains in cotton blue in lactophenol), compared with about 90 percent in most nonhybrid individuals. In meiosis, they formed 7 pairs of chromosomes, including 6 ring bivalents, indicating nearly complete homology between the chromosomes of the parental plants.

2. Camissonia angelorum (S. Wats.) Raven, Brittonia 16: 283. 1964.

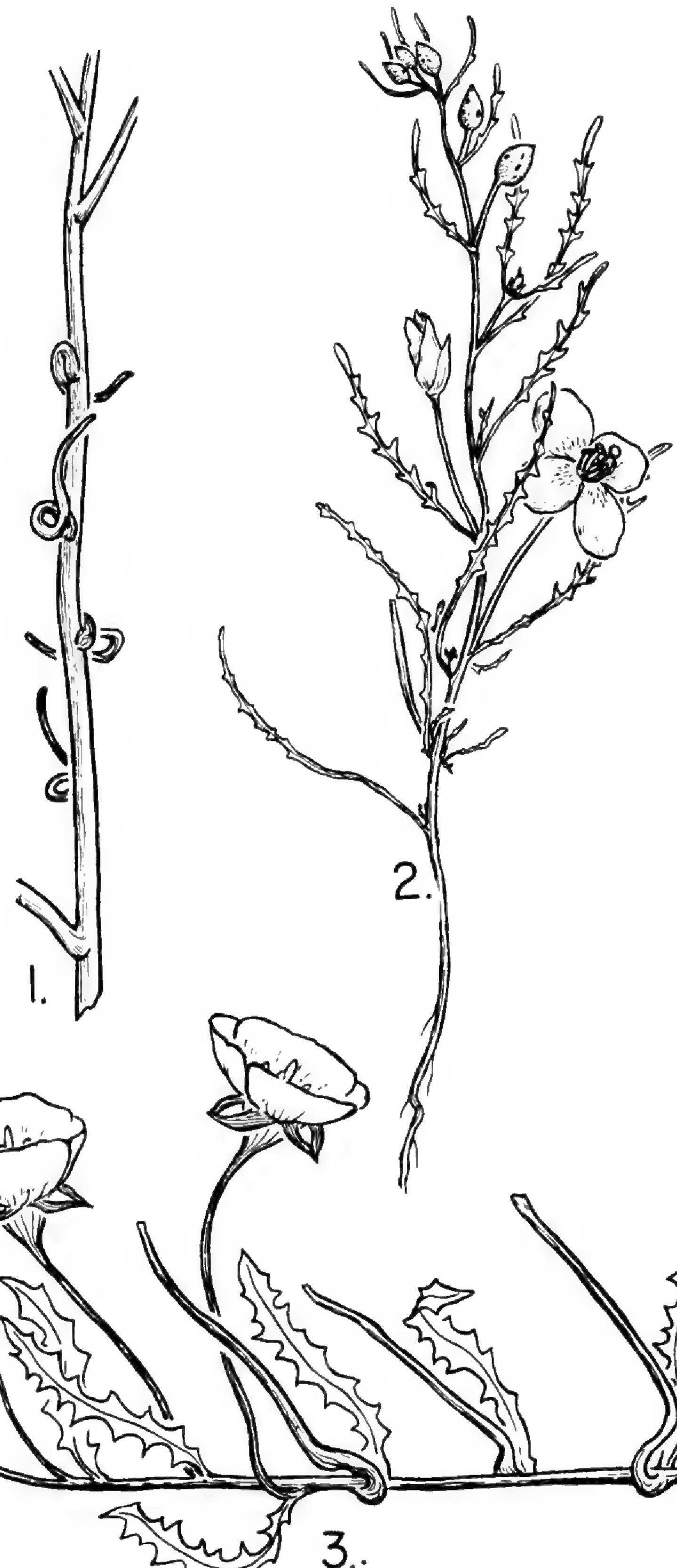
Figures 1, 2

Oenothera angelorum S. Wats., Proc. Amer. Acad. 24: 49. 31 January 1889.

Oenothera crassiuscula Greene, Pittonia 1: 290. 16 April 1889. Type: Low plains around the southern shore of Bahía de San Bertólome, Baja California, March 1889, *Lieutenant Pond* (location of specimen not known).

Sphaerostigma angelorum (S. Wats.) A. Nels., Bot. Gaz. 40: 63. 1905.

Erect, sparingly branched, virgate annual 8–90 cm. tall, with no distinct basal rosette, not flowering at the basal nodes, glabrous or sparsely strigulose, the inflorescence strigulose. Leaves deeply pinnatifid, very narrowly elliptic, 1–7.5 cm. long, 1–15 mm. wide, the apex acuminate, the base attenuate; leaves subsessile or with a petiole up to 3 mm. long. Inflorescence long and virgate. Hypanthium 3–4.2 mm. long, 3–4.5 mm. across at the summit, sparsely pubescent or subglabrous in lower half within. Sepals 6.5–11 mm. long, 1.2–2.2 mm. wide, reflexed in pairs or groups of 3 or 4. Petals 10–19 mm. long, 8–21 mm. wide, finely flecked with red in basal third. Filaments of the



FIGURES 1–3.—Species of *Camissonia* sect. *Eulobus*, × ¾: 1–2, *C. angelorum*: 1, Portion of a fruiting branch (*Wiggins* 18189, DS); 2, a flowering plant (*Wiggins & Thomas* 299, DS). 3, Flowering branch of *C. sceptrostigma* (*Wiggins* 16824, DS).

episepalous stamens 3–5 mm. long, those of the epipetalous ones 2–3.5 mm. long; anthers 2–3.2 mm. long, long-ciliate. Style 5–9 mm. long, subglabrous or with scattered erect trichomes near its base; stigma globose, 1.3–2 mm. thick, held at the level of the anthers of the longer stamens at anthesis, or perhaps a little above them in certain plants. Capsules contorted, but often not as much so as in *C. crassifolia*, 1.5–3.5 cm. long, 1–1.4 mm. thick. Seeds as in *C. crassifolia*. Gametic chromosome number, $n=7$. Self-compatible and capable of self-pollination, but probably often outcrossed in nature.

TYPE: Bahía de los Angeles, Baja California, 22 November to 20 December 1887, *E. Palmer* 519 (GH; isotypes, BM, C, K, NY, UC, US).

DISTRIBUTION (Figure 4): Sandy flats and washes in Baja California, ranging across the peninsula, from the vicinity of Punta Final on the gulf coast at about 29°45′ N. lat. south to the northern edges of the Desierto Vizcaíño at about 27°40′ N. lat.; also on Isla San Lorenzo in the Golfo de California. From sea level to about 1,500 ft. alt.

Vouchers for chromosome number (9 individuals, 9 populations), $n=7$ (all with 7 pairs):

BAJA CALIFORNIA: 2 mi. inland from Ensenada de San Francisquito, *Moran* 12391 (DS, SD); 17 mi. S. of Laguna Seca Chapala, *Thorne & Hendrickson* 32640 (DS, RSA); Salorio, *Moran* 12314 (DS, SD); ca. 10 mi. E. of Bahía de los Angeles, ca. 1,500 ft., *Wiggins* 14808 (DS, progeny); Bahía de los Angeles, *Moran* 12298 (DS, SD); just N. of San Borja, *Moran* 12461 (DS, SD); Bahía de San Francisquito, *Moran* 12618 (DS, SD); Arroyo Salinito, *Moran* 12860 (DS, SD); El Datillar, 8 mi. N. of Rancho Miramar, *Moran* 12847 (DS, SD).

REPRESENTATIVE SPECIMENS EXAMINED:

BAJA CALIFORNIA: 25 mi. N. of Rancho Laguna Chapala on road to San Felipe, 1,130 ft., *Wiggins & Ernst* 662 (DS, UC); just W. of Bahía de San Luis Gonzaga, *I. L. & D. B. Wiggins* 15906 (DS); 25 mi. N. of Punta Prieta, *Wiggins* 5361 (CAS, DS, GH, NY, POM, RM, UC, US, WTU); 20 mi. E. of Punta Prieta, *Wiggins* 7662 (DS, GH, UC, US); Bahía de Los Angeles, *Wiggins* 7692 (DS, GH, LA, UC, US); near San Andreas, *Wiggins & Thomas* 215 (DS); 18 mi. S. of Punta Prieta, *I. L. & D. B. Wiggins* 18189 (CAS, DS); 12 mi. NE. of Rancho Rosarito on road to San Borja, *Porter* 559 (CAS, DS, GH, RSA); Bahía de San Francisquito, *Johnston* 3572 (CAS, GH, K, US); Rancho Barril, *Wiggins* 7822 (DS, F, GH, US); Laguna de Guerrero Negro, *Thomas* 8508 (DS); 21 mi. E. of Laguna de Guerrero Negro on road to El Arco, *Wiggins* 16828 (DS); 40 mi. inland from Lagoon Head, 1889, *Palmer* 771 (GH, K, POM, US); 8 mi. W. of Calmallí, *Haines & Stewart* in 1935 (ARIZ, DS, GH, K, LA, NY, POM, RM, RSA, UC, WTU); El Cañon Rancho near Calmallí, *Haines & Stewart* in 1935 (ARIZ, DS, F, GH, K, LA, POM, RM, RSA, UC); 7 mi. SE. of Rancho La Cantina, *Wiggins* 16209C (DS); Bahía de San Bertólome, *Rose* 16208 (GH, US); 5.5 mi. N. of El Huizache, Vizcaíño Desert, *Porter* 541 (CAS, DS, RSA). SOUTH SAN LORENZO ISLAND: *Moran* 4130 (DS, UC).

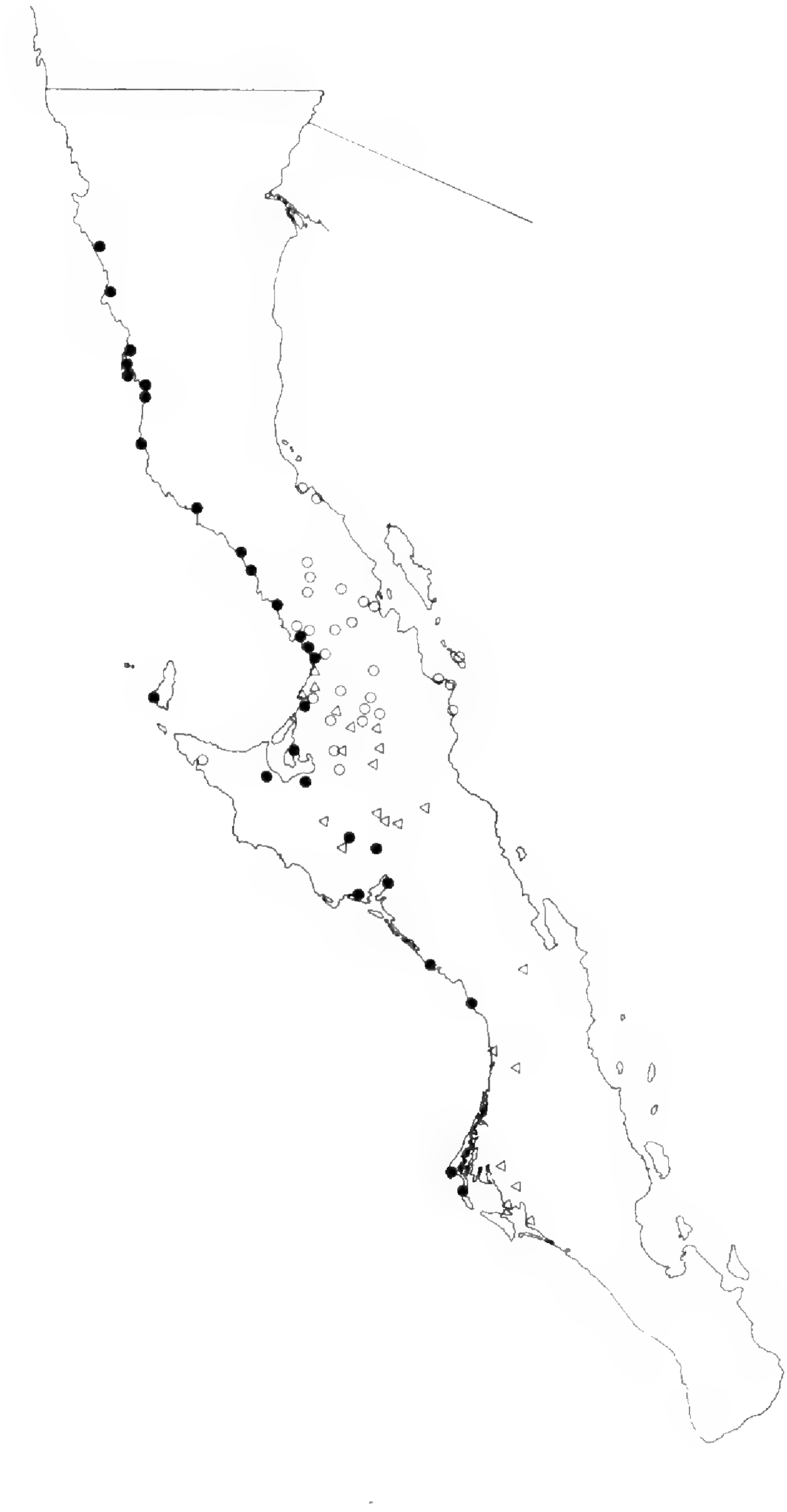


FIGURE 4.—Baja California, showing ranges of *Camissonia* sect. *Eulobus:* ●=*C. crassifolia;* ○=*C. angelorum;* △=*C. sceptrostigma.*

The collection cited from Bahía de San Bertólome has deeply cut leaves and very probably is similar to the unlocated type of *Oenothera crassiuscula*, from the same region. *Camissonia angelorum* is rather obviously an annual derivative of *C. crassifolia* and certain populations, notably some to those from the Desierto Vizcaíño region at the southern limits of *C. angelorum*, can be assigned to one species or the other only with the greatest difficulty. The two species might be regarded as geographical subspecies, but the shift in breeding system and ensemble of morphological features distinctive of each are sufficient to make their continued recognition as species desirable, in my opinion. Progeny of *Wiggins* 14808, grown at Stanford, set seed abundantly in the absence of insects and when isolated from one another; nevertheless, the showy flowers of *Camissonia angelorum* suggest strongly that this species must at least occasionally be cross-pollinated by insects in nature. *Camissonia angelorum* has been observed growing sympatrically with tetraploid populations of *C. californica*.

3. Camissonia sceptrostigma (T. S. Brandeg.) Raven, Brittonia 16: 283. 1964.

FIGURE 3

Oenothera sceptrostigma T. S. Brandeg., Proc. Calif. Acad. II. 2: 156. 1889.

Rosette-flowering annual, with prostrate branches tardily elongating from the base, these to at least 35 cm. long, with the leaves, flowers, and capsules standing erect from them; entire plant finely strigulose, often grayish-pubescent. Leaves thin, deeply and irregularly pinnatifid with narrow lobes, narrowly elliptic, 1.5–16 cm. long, 4 27 mm. thick, the apex acuminate, the base attenuate. Hypanthium 3.2–6 mm. long, 2.5–5 mm. across at the summit, glabrous within. Sepals 3–8.5 mm. long, 1–2.4 mm. wide, spreading (not reflexed), separate from one another. Petals 6.5–17.5 mm. long, 8–19 mm. wide, with diffuse red flecking near the base. Filaments of the episepalous stamens 1.7–4.5 mm. long, those of the epipetalous ones 0.8–1.8 mm. long; anthers 1.2–2.5 mm. long, glabrous or finely pubescent, held erect. Style 3.5–8.3 mm. long, glabrous; stigma cylindrical, 1.4–4.5 mm. long, 0.4–1.2 mm. thick, held ± above the anthers at anthesis. Capsules in the rosette straight or nearly so, those of the branches somewhat flexuous, 1.7–4 cm. long, 1.5–1.8 mm. thick. Seeds 0.8–1.2 mm. long, 0.4–0.6 mm. thick, pale brownish, not spotted. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: San Gregorio, Baja California, 1 February 1889, *T. S. Brandegee* (CAS; isotypes, DS, PH, US).

DISTRIBUTION (Figure 4): Sandy fields and washes in central and southern Baja California, from 11 miles south of Millers Landing, at about 28°20′ N. lat., to the south end of Bahía de la Magdalena, at about 24°30′ N. From near sea level to ca. 1,200 ft. alt.

Voucher for chromosome count (2 individuals, 2 populations; $n=7$):

BAJA CALIFORNIA: 3¼ mi. W. of Rancho Miramar, 28°08′ N. lat., 113°40′ W. long., ca. 150 m, *Moran* 12857 (DS, SD); *Verity* in 1967 (R68–302; DS).

ADDITIONAL SPECIMENS EXAMINED:

BAJA CALIFORNIA: 11 mi. S. of Millers Landing, *Wiggins* 15099 (DS); 3 mi. W. of main road and ca. 4–5 mi. N. of Rancho Mesquital, *Wiggins* 16768 (DS); 24 mi. E. of Laguna de Guerrero Negro, *Wiggins* 16824 (DS); Lagoon Head, 1889, *Palmer* 772 (C, CAS, GH, K, NY, UC, US); 23.2 mi. NW. of El Arco, *Porter* 207 (DS, GH); 11 mi. W. of El Arco, *Wiggins* 1683A (DS); El Arco, *Epling & Robinson* in 1935 (DS); 10 mi. E. of El Soltero, *Wiggins* 15148 (DS); 15 mi. S. of El Arco, *Wiggins* 15156 (DS, UC); 22 mi. S. of Pozo Alemán, *Wiggins* 7849 (DS, F, GH, UC, US); Arroyo de Tecolote, Desierto Vizcaíño, *Gentry* 7835 (ARIZ, DS, UC); Picachos de Santa Clara, Desierto Vizcaíño, *Gentry* 7759 (ARIZ, DS, UC); 5–7 mi. E. of Los Picachos de Santa Clara, *Gentry* 7593 (RSA, UC); 15 mi. E. of El Soliyo, *Wiggins* 15148 (UC); 7 mi. S. of Los Angeles, San Ignacio to El Arco road, *Wiggins & Ernst* 626 (DS, UC); E. edge of Desierto Vizcaíño, 56 km. S. of El Arco, *Carter et al.* 1940 (SD); 40 mi. W. of San Ignacio, *Hake* in 1921 (DS); 50 km. NW. of San Ignacio, *Carter et al.* 1960 (DS, F, GH, K SD, US); 25 mi. N. of San Ignacio, *Wiggins & Ernst* 615 (DS, UC); 14 mi. N. of San Ignacio, *Reed* 6203 (POM); 24 mi. N. of La Purísima, *Wiggins & Ernst* 589 (DS, UC); Punta San Juanico, *Moran* 3524 (DS); Santo Domingo, *Orcutt* (UC); San Jorge, *Gentry* 4176 (DS); 51 mi. NW. of El Crucero, *Porter* 488 (CAS, DS, GH); 10 km. N. of Medano Amarillo, Bahía de la Magdalena, *Johansen* 644 (CAS, DS); S. of El Refugio, *Wiggins* 5526 (DS); 14 mi. S. of El Refugio, *Shreve* 7179 (ARIZ, DS, F); Estero Salinas, *Porter* 462 (CAS, DS, GH, UC), *Wiggins* 11477 (DS, GH UC, US); Bahía de la Magdalena, *Lung* in 1894 (UC).

Camissonia sceptrostigma is uniform morphologically and, while an undoubted member of sect. *Eulobus*, is entirely distinct within the group. It has not been observed growing sympatrically with any of the other three species of the section, but occurs in the same vicinity as each one of them in the region of the northern Desierto Vizcaíño. Four plants of the Verity collection cited above were grown in the experimental garden and found to be self-incompatible.

4. Camissonia californica (Nutt. ex Torr. & Gray) Raven, Brittonia 16: 283. 1964.

Eulobus californicus Nutt. ex Torr. & Gray, Fl. N. Amer. 1:515. 1840. Not *Oenothera californica* S. Wats. 1876.

Oenothera leptocarpa Greene, Pittonia 1: 302. 1889.

Oenothera eulobus H. Lév., Monogr. Onoth. 231. 1905.

Oenothera crassifolia var. *leptocarpa* (Greene) H. Lév., Monogr. Onoth. 209 1905.

Virgate annual 2–180 cm. tall, with a well-defined basal rosette which is usually withered by the time of flowering; no flowers formed in the lower nodes; stems thick, fleshy, hollow, bluish green, sometimes glaucescent, or bright green. Plants subglabrous, the leaves occasionally finely strigulose or with a few glandular trichomes on the margins and midvein. Leaves irregularly and sharply pinnatifid-lobed, very much reduced upward and in the inflorescence, mostly in the basal

rosette, narrowly elliptic, up to 30 cm. long and 6.5 cm. wide, the apex acute, the base narrowly cuneate. Inflorescence with a few glandular trichomes, very rarely strigulose. Hypanthium 0.6–1.5 mm. long, 1–1.8 mm. across at the summit, glabrous within, closed by a conspicuous rounded fleshy disc. Sepals 3.9–8 mm. long, 0.7–1.5 mm. wide. Petals 6–14 mm. long, 3.5–8.5 mm. wide, with or without fine red flecking at the base. Filaments of the episepalous stamens 3–9 mm. long, those of the epipetalous ones 2–5 mm. long; anthers of longer stamens 1–2.5 mm. long, those of the shorter ones greatly reduced 0.5–1.2 mm. long. Style 4–10 mm. long, glabrous; stigma 0.8–2 mm. thick, held at the same level as the anthers of the longer stamens, which more or less surround it at anthesis. Capsules straight or slightly curved, (4.5–) 6–11 cm. long, 1–1.2 mm. in diameter, subterete when fresh, becoming quadrangular in transection when dry, sharply reflexed at maturity. Seeds 1.3–1.6 mm. long, 0.5–0.7 mm. thick, olive, often flecked with purple dots. Gametic chromosome numbers, $n=7$, 14. Mostly self-pollinating, and apparently always self-compatible; rarely visited by insects.

TYPE: Near San Diego, San Diego County, California, March–May 1836, *T. Nuttall* (NY; isotypes, BM, GH, K, PH).

DISTRIBUTION (Figure 5): Open or brushy hillsides and washes, or desert flats, often in loose soil: upper Austin Creek, Sonoma County, California (*Kruckeberg* 5933, DS); from the southern half of San Benito County and westernmost Fresno County, California, south through the Coast Ranges and mountains of southern California; the low foothills for about 20 miles east of Bakersfield, Kern County, California; and across the deserts (common along their western margins; absent in the Colorado Desert east of the Salton Sink; rare in the Providence and Old Woman Mountains of the eastern Mojave Desert) to western and southern Arizona (vicinity of Kingman, Mohave County; southernmost Yavapai, Gila, and Graham Counties southward); whence south to central Sonora (to ca. 7 miles west of Mina San José on road to Misa, *Wiggins* 6317, DS, POM, US; north of Bocoachic, 3,730 ft., *Wiggins* 11704, DS) at about 28°20′ N. lat. and throughout Baja California south to the Sierra Vizcaíño at about 27°15′ N. lat. (e.g., *Gentry* 7416, DS, POM; *Gentry* 7515, DS); also on Santa Cruz and Santa Catalina Islands, California. From sea level to 4,000 ft. alt.

Vouchers for chromosome number (39 individuals, 24 populations), $n=7$:

U.S.: CALIFORNIA: LOS ANGELES CO.: Santa Monica Mts.: Decker Canyon, *Mathias* 3159 (COLO, LA, RSA, UC); Latigo Canyon, *Venkatesh* 6 (3 plants; LA), 7 (2 plants; ARIZ, LA, RSA, UC); South Sepulveda Way, *Lewis* 1629 (LA); Mulholland Drive, 6.3 mi. from intersection with Beverly Glen Blvd., *Venkatesh* 4 (LA), 2.5 mi. from intersection, *Venkatesh* 2 (11 plants; LA). ORANGE CO.: 2.3 mi. above gate on Silverado Canyon Truck Trail, R17749. RIVERSIDE CO.: 3.5 mi. W.

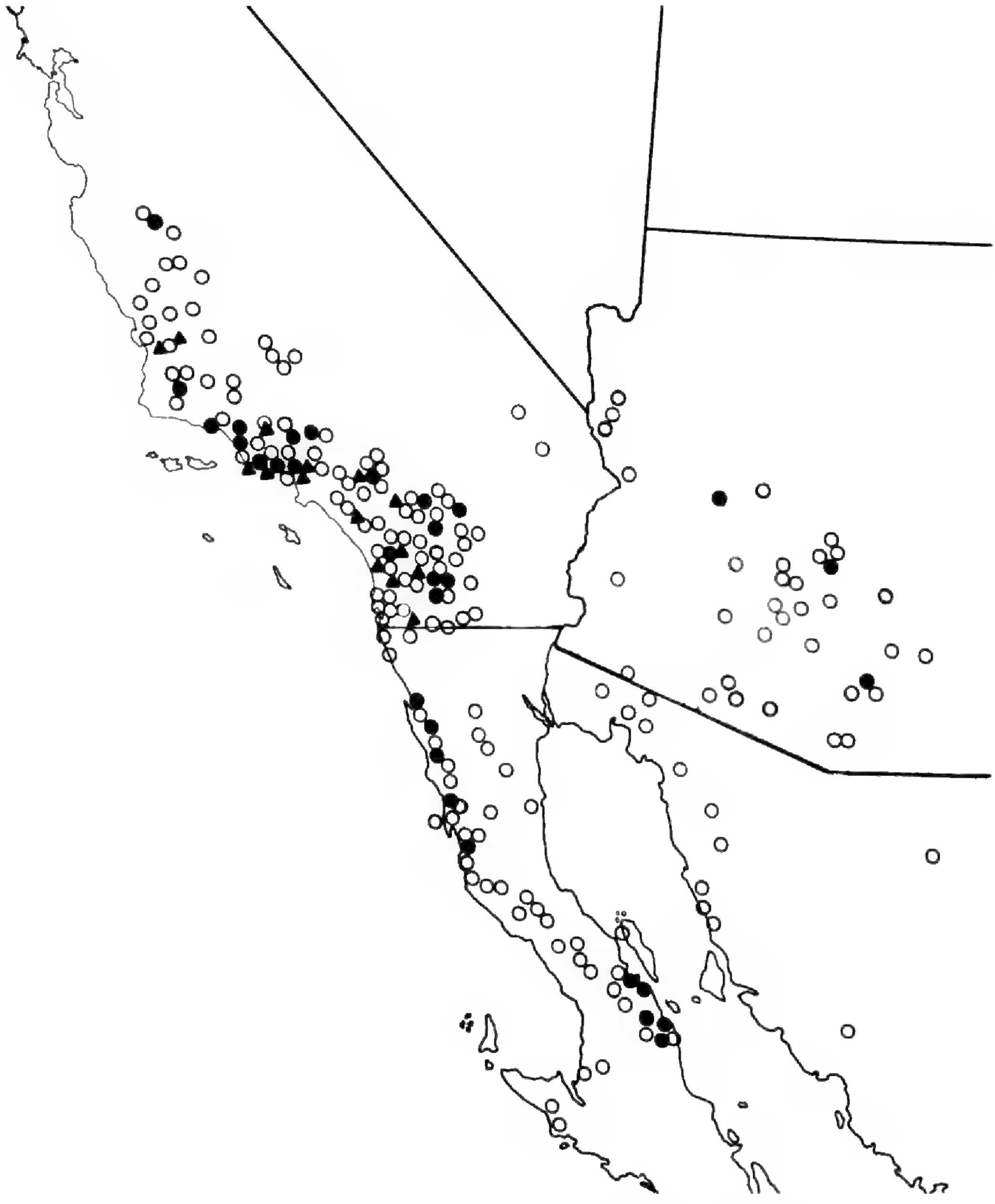


FIGURE 5.—Portion of southwestern United States and adjacent Mexico, showing range of *Camissonia californica* (O): ▲=diploid chromosome counts ($n=7$) and ●=tetraploid ($n=14$).

of Cabazon, *Lewis* 1679 (LA); 2 mi. N. of Aguanga, *Klein* 1299 (RSA). SAN BERNARDINO CO.: N. of Muscovy, *Gregory* 362 (RSA). SAN DIEGO CO.: 2.3 mi. S. of Rincon Springs, R17399; Lake Wohlford, R20170; 2 mi. E. of Escondido, 700 ft., R17405; 2 mi. E. of San Pasqual, R17410; Rincon Springs, R20172; 1.8 mi. from Ballena on road to Ramona, R9581 (LA); 0.7 mi. W. of Banner, 3,000 ft., R17421; 0.9 mi. W. of Barrett Lake Road on State Hwy. 94, *Breedlove* 1832. SAN LUIS OBISPO CO.: Parkhill Road, Calf Canyon, La Panza Campground, ca. 2,000 ft., R18325; La Panza Campground, 2,100 ft., R18324; 4.5 mi. NE. of Santa Margarita, R20157. VENTURA CO.: 11.4 mi. N. of Fillmore on Cow Springs Road, Topatopa Mts., 2,500 ft., *Breedlove* 2653; 9 mi. S. of Oxnard, State Hwy. 101A, *Copp in 1962*.

BAJA CALIFORNIA: Ensenada, *Bates* 2340.

Vouchers for chromosome number (53 individuals, 38 populations), $n=14$:

U.S.: ARIZONA: MARICOPA CO.: 12 mi. SW. of Roosevelt, *Gregory* 61 (RSA). PIMA CO.: Santa Catalina Mts.: 2.8 mi. below Molina Basin Picnic Area, *Lewis* 1075 (LA); Molina Basin Picnic Area, *Lewis* 1077 (LA, RSA). YAVAPAI CO.: 2 mi. E. of Congress Junction, *Munz et al.* 22972 (RSA). CALIFORNIA: LOS ANGELES CO.: Soledad Canyon, *Lewis & Thompson* 1615 (LA); Mint Canyon at road to Acton, R13906. SANTA MONICA MTS.: Latigo Canyon, R20162; 2.5 mi. W. of Seminole Hot Springs, R20163; 4.1 mi. NW. of Tapia Park, R14046; Topanga Canyon, *Venkatesh* 5 (8 plants; LA); Mulholland Drive 1.3 mi. W. of Laurel Canyon Blvd., R14081 (COLO, LA, RSA); Mulholland Drive 6.3 mi. from junction with Beverly Glen Blvd., *Venkatesh* 3 (6 plants; LA). RIVERSIDE CO.: Aqueduct Road 5.9 mi. S. of Garnet, *Lewis* 1620 (LA); Pinyon Crest Road 2.5 mi. from Palms-to-Pines Hwy., *Theobald* 61; Pushawalla Canyon, *H. & M. Lewis* 1610 (LA). SAN BENITO CO.: Call Mts., E. of a point 18 mi. N. of New Idria, R10875 (LA, RSA). SAN BERNARDINO CO.: 1.5 mi. W. of Mill Creek Ranger Station, R17468; Morongo Valley, *Kyhos* 65–125. SAN DIEGO CO.: 0.4 mi. from U.S. Hwy. 395 on road to Fallbrook, *Wedberg* 205 (herb. San Diego State College); Earthquake Valley, R11537; Borrego Valley, *H. & M. Lewis* 1544 (LA); 0.7 mi. W. of summit of Yaqui Pass, R11520. SANTA BARBARA CO.: Head of Buckhorn Canyon, summit of San Rafael Mts., on Tepusquet Canyon Road, *Breedlove* 2780; Santa Barbara, *Breedlove* 2227; 1 mi. S. of Prisoners Harbor, Santa Cruz I., *Breedlove* 2816. VENTURA CO.: 0.5 mi. N. of turn to Matilija Hot Springs, 1,400 ft., R17495; 0.3 mi. SW. of Camp Comfort, S. of Ojai, 600 ft., R17494; Little Sycamore Canyon, Santa Monica Mts., *Lewis* 1646 (LA).

BAJA CALIFORNIA: 7.5 mi. N. of Santa Tomás, R17049; 5.5 mi. S. of San Vicente, R17023; 5 km. N. of Colonia Guerrero, R12152 (LA, UC); 2 km. N. of Colonia Guerrero, R12142 (LA, UC); 14 mi. S. of San Quintín, R17031; 7.5 mi. S. of Socorro, *Klein* 1222 (RSA); 2 mi. inland from Ensenada de San Francisquito, *Moran* 12392; Bahía de los Angeles, *Moran* 12308; Las Trincheras, *Moran* 12608; Cuesta la Ley, Barril road, *Moran* 12642.

Camissonia californica, with its virgate habit, nearly leafless branches, and long, sharply reflexed capsules, superficially resembles some species of Cruciferae more than members of the family Onagraceae. Its capsules have been said to be imperfectly 4-celled, or 2-celled as in the related genus *Gayophytum* (Munz, Amer. Journ. Bot. 16: 253–254. 1929; N. Amer Fl. II. 5: 80. 1965), but I have been unable to confirm this in the wide range of material examined. This species, while very distinct, is obviously closely related to the other three grouped with it by Munz (loc. cit.) and recognized in the present revision as comprising *Camissonia* sect. *Eulobus*. It has been observed growing sympatrically with *C. crassifolia* and *C. angelorum*, but no hybrids have been found.

The only tetraploids in sect. *Eulobus* are found in the present species. I have found no character or combination of characters by which they can be separated from the diploids, and their pollen appears to be identical in size and number of pores. As pointed out by Munz (N. Amer. Fl. II. 5: 146. 1965), coastal populations of this species tend to consist of relatively robust, large-flowered plants; yet it is by no

means true that all such populations are diploid. On the basis of the 92 individuals and 62 populations reported here (including earlier reports by Lewis et al., Aliso 4: 73–86. 1958), the diploids are much more narrowly distributed than the tetraploids (fig. 5). Diploids are known from coastal San Luis Obispo County, and occur sporadically near the coast in Ventura and Los Angeles Counties. From the Los Angeles basin to San Diego County, they range much farther inland, occurring to the margin of the desert near San Gorgonio Pass and near Aguanga; but they are intermixed with tetraploid populations in some pattern not yet properly understood, occurring as far west as the vicinity of Fallbrook in northwestern San Diego County. Unfortunately, no counts are available for extreme western Riverside County or for Orange County. In San Diego County, aside from the Fallbrook record just mentioned, most of the populations appear to be diploid, the tetraploid being confined to the margins of the desert. In Baja California, on the other hand, only a single diploid count is known, that from Ensenada, and all of the interior populations and those near the coast farther south (which consist of robust, large-flowered individuals similar to the coastal ones found farther north) are tetraploid. There does not appear to be any point in attempting to separate the diploid and tetraploid populations of this species taxonomically, and indeed there does not seem to be any practical possibility of doing it even if it were thought to be highly desirable.

No multivalent configurations have been observed in the tetraploid, but the lack of chromosome associations larger than bivalents is undoubtedly genetically controlled, as it is in sect. *Holostigma* and sect. *Camissonia*, and certainly does not indicate a complete lack of homology between the two sets of chromosomes present in these tetraploid populations. Indeed, an autotetraploid origin appears most likely for these tetraploids and would be consistent with their morphological relationships. If this is true, however, it is somewhat difficult to explain the occurrence of the tetraploids over a much wider range than the diploids, unless one could postulate that they recombine the genetic material present in diploid populations in some novel way (or ways) highly adaptive in more interior sites. This favorable genetic combination could be maintained by the tetraploidy of the interior plants, which are probably also more highly self-pollinating than those found nearer the coast, judging from their smaller flowers. Two diploid populations (R20157, cited above, from San Luis Obispo County, California, 7 plants; and R20166, San Pasqual Grade, San Diego County, California, 8 plants) and three tetraploid populations (Morongo Valley, San Bernardino County, California, *Kyhos* 65–125, 2 plants; Santa Monica Mountains, Los Angeles County, California, R20162, 5 plants; R20163, 6 plants the last two cited above)

were tested by pollen-tube growth and found to be self-compatible. *Kruckeberg* 5933, cited above, was grown in a greenhouse at the University of Washington and found also to be self-compatible (A. R. Kruckeberg, pers. comm.). This collection was undoubtedly also tetraploid. In the smaller flowered interior populations, the anthers deposit pollen directly on the stigma and there is no doubt that autogamy predominates.

The disjunct occurrence of this species on serpentine near Austin Creek in western Sonoma County, California, is of considerable interest. I have no record of its occurrence on serpentine elsewhere, but it is characteristic for species occurring in highly marginal situations to occur in edaphic conditions that are unusual or unknown in their main area of distribution (Raven, Evolution 18: 336–338, 1964).

Section II. *Chylismia*

Camissonia sect. *Chylismia* (Nutt. ex Torr. & Gray) Raven, Brittonia 16: 281 1964.

Oenothera subg. *Chylismia* Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 506. 1840.

Chylismia (Nutt. ex Torr. & Gray) Raimann, *in* Engl. & Prantl, Natürl. Pflanzenfam. III. 7: 217. 1893.

Oenothera sect. *Euchylismia* (Nutt. ex Torr. & Gray) Munz, Amer. Journ. Bot. 15: 224. 1928.

Oenothera sect. *Chylismia* Raven, Univ. Calif. Publ. Bot. 34: 80. 1962.

Oenothera sect. *Tetranthera* Raven, Univ. Calif. Publ. Bot. 34: 114. 1962.

Type species: *Oenothera exilis* Raven = *Camissonia exilis* (Raven) Raven.

Camissonia sect. *Tetranthera* (Raven) Raven, Brittonia 16: 282. 1964.

Perennial or annual herbs, the plants caulescent, not flowering at the basal nodes, with or without a well-developed basal rosette. Leaves pinnately divided or entire. Inflorescence erect or drooping in bud. Flowers opening near sunrise or in the late afternoon (in *C. claviformis* only). Ovary lacking a sterile projection. Hypanthium lacking a fleshy disc within. Sepals reflexed separately. Petals yellow, white, or lavender, if yellow strongly ultraviolet reflective, with or without one or more red dots near the base, and some yellow-flowered species[2] with the basal area of the petals with a large, nonultraviolet reflective area; petals, if white or yellow, often fading orange red after pollination. Stamens 8 or 4; anthers versatile, long-ciliate or glabrous. Pollen shed singly. Capsule long-pedicellate, regularly and promptly loculicidal, each valve with a brown, prominent midrib, terete, the seeds in 2 rows in each locule. Seeds monomorphic, lenticular, with a more or less pronounced membranous margin when immature, lance-ovoid when mature, finely lacunose.

Type species: *Camissonia scapoidea* (Torr. & Gray) Raven.

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[2] *Camissonia brevipes*, *C. confertiflora*, *C. eastwoodiae*, and *C. multijuga*. Other species did not show a contrasting pattern of this sort.

DISTRIBUTION: Sandy desert slopes, flats, and washes, often with *Artemisia tridentata* in the northern part of its area, or on rock slides or cliffs, from southeastern Oregon, east-central and southern Idaho, and central and western Wyoming, south throughout the Great Basin in eastern California, Nevada, and western Colorado, to northwesternmost New Mexico, throughout Arizona, and widespread in the Mojave and Colorado Deserts, south to northwesternmost Sonora above the head of the Golfo de California, and in eastern Baja California south to the vicinity of Bahía de los Angeles at about 29° N. lat. Also, *Camissonia scapoidea* has been collected twice on the upper drainage of the Arkansas River in eastern Colorado and is the only species of its section and one of the two in the genus—the other is *C. chamaenerioides*—to occur east of the crest of the southern Rocky Mountains. Plants of *Camissonia* sect. *Chylismia* do not occur west of the Cascade-Sierra Nevada axis and constitute the only major group of the genus strictly confined to the deserts; however, the distribution of sect. *Eremothera* is generally similar.

The phylogeny and relationships of this group were discussed by me in detail in 1962 (Univ. Calif. Publ. Bot. 34: 1–122), and the section is included here only to bring it into line with my treatment of the rest of the genus and to bring my account of it up to date. The only specimens cited in the present treatment are types and recently collected vouchers for chromosome number determinations and range extensions. Distribution maps were presented in my 1962 revision and are not reprinted here.

Only one major change is made in the present treatment. Impressed with its loss of the epipetalous stamens, I set up a new monotypic section, sec. *Tetranthera*, for *Camissonia exilis* in my 1962 revision. Subsequently, however, I have found that some individuals of *C. andina* (sect. *Nematocaulis*) likewise have lost the epipetalous stamens, and some individuals of *C. minor* (sect. *Eremothera*) approach this condition. In all of these cases, the loss of this whorl of stamens appears to be associated with autogamy. In the light of this information, and considering the close overall resemblance between *C. exilis* and *C. walkeri*, *C. scapoidea*, and *C. parryi*, I now feel that my earlier segregation of *C. exilis* as a monotypic section reflected an unwarranted overemphasis of a single characteristic. The relationships of this species appear to be reflected more accurately when it is included in sect. *Chylismia* with its close relatives.

5. Camissonia confertiflora (Raven) Raven, Brittonia 16: 281. 1964.

Oenothera confertiflora Raven, Univ. Calif. Publ. Bot. 34: 80. 1962.

Stout annual herb 15–50 cm. tall, branched at the base and above, with a well-developed basal rosette; stems densely villous at the base, mixed with shorter strigose pubescence, and villous above with short

glandular pubescence. Basal leaves oblanceolate, 7–20 cm. long, pinnate, the lateral leaflets to 2 cm. long, alternating with shorter pinnules, or reduced; terminal leaflet narrowly ovate, to 5 cm. long and 2.5 cm. wide, sparsely villous. Inflorescence dense and corymbiform in bud, later elongating, glandular-puberulent. Hypanthium 3-5 mm. long, 3–5 mm. across at the summit, short-villous within below. Sepals 9–12 mm. long, 2.5–4 mm. wide, glandular-pubescent, or with a few scattered long trichomes; free caudate portions conspicuous, arising just below the apices, these with a median row of light brown oil cells. Petals 12–18 mm. long, 12–17 mm. wide, bright yellow, of same color as stamens, style, and inside of hypanthium, red dotted at the base, fading purplish. Filaments of the episepalous stamens 6–8 mm. long, those of the epipetalous ones 4–5 mm. long; anthers 4–6 mm. long, ciliate. Style 11–18 mm. long; stigma ca. 1.5 mm. thick, held well above the anthers at anthesis. Immature capsule to 35 mm. long, on a pedicel 5–15 mm. long, glandular-pubescent. Seeds not known. Presumably self-incompatible.

TYPE: In cinder soil, on east side, base of Vulcan's Throne, Toroweap Valley, ca. 4,200 ft., Grand Canyon National Monument, Mohave County, Arizona, 30 April 1952, *E. McClintock* 52–294 (CAS 373481; isotypes, ARIZ, NY, WS).

DISTRIBUTION: Known only from the type locality.

Camissonia confertiflora is most closely related to *C. brevipes* and to *C. multijuga*. It is easily distinguished from the latter by its larger flowers, drooping inflorescence, and large buds; and from the former by its glandular sepals, unequal stamens, and uniformly branched habit. In addition, the single locality for *C. confertiflora* is outside the range of *C. brevipes*. *Camissonia multijuga* grows within less than a mile of this locality, but in this area is very distinct; some collections, however, such as one from Searchlight Ferry, Mohave County, Arizona (*Shreve* 7870), are more similar to *C. confertiflora* in their crowded inflorescences and larger flowers. No more is known about this species at present than when I described it in 1962.

6. Camissonia brevipes (A. Gray) Raven, Brittonia 16: 281. 1964.

Annual, 3–75 cm. tall, the stems often densely clothed below with spreading white trichomes. Leaves mostly in a basal rosette, spatulate, the terminal leaflet to 6.5 cm. long and 5 cm. wide, sometimes cordate at the base, the lateral leaflets reduced or absent. Inflorescence nodding, elongating in flower and fruit. Hypanthium 3–8 mm. long, densely short-villous in lower portions within, 1.5–7 mm. across at the summit. Sepals 5–9 mm. long, the apices covered with brown oil cells, the caudate appendages present or absent. Petals 3–18 mm. long, 4–25 mm. wide, bright yellow, rarely red dotted, the same color as the stamens and style. Stamens subequal; filaments 3–6 mm. long;

anthers 2.5-6 mm. long, ciliate. Style 10–18 mm. long; stigma 1–2 mm. thick held above the anthers at anthesis. Capsule 18–92 mm. long, glabrous or sparsely villous, ascending or spreading, straight or curved; pedicel 2–20 mm. long. Seeds 1–1.5 mm. long, 0.6–1 mm. wide. Gametic chromosome number, $n=7$. Self-incompatible.

DISTRIBUTION: Alluvial slopes, flats, and canyon sides, Washington County, Utah, Lincoln and Esmeralda Counties, Nevada, and Inyo County, California, south to Yuma County, Arizona, and Imperial County, California. From ca. 230 ft. below sea level to 6,000 ft. alt.

6a. Camissonia brevipes subsp. **brevipes** FRONTISPIECE

Oenothera brevipes A. Gray, Pac. R. R. Rept. 4: 87. 1857.

Oenothera divaricata Greene, Bull. Torrey Cl. 10: 125. 1883. Type: CAS 866, labeled: "The specimen found among the 'Cruciferae' of State Geo. Survey"; isotype, GH. As indicated in a note penciled by Katherine Brandegee, probably the same as a specimen from gravelly banks, Fort Mojave, Mojave County, Arizona, 15 February 1861, *J. G. Cooper* (GH), bearing the characteristic printed label, "Geological Survey of California 1860–61."

Chylisma brevipes (A. Gray) Small, Bull. Torrey Cl. 23: 194. 1896.

Oenothera brevipes var. *typica* Munz, Amer. Journ. Bot. 15: 228. 1928.

Oenothera brevipes subsp. *brevipes;* Raven, Univ. Calif. Publ. Bot. 34: 81. 1962.

Stout, generally unbranched above, the stems villous. Terminal leaflet ovate. Inflorescence dense, nodding. Hypanthium 4–8 mm. long, villous without, yellow within. Sepals usually villous, with a caudate protection arising below the apex. Petals 6–18 mm. long, 7–25 mm. wide. Anthers 4–6 mm. long. Capsule 20–92 mm. long; pedicel 5–20 mm. long. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: On gravelly hills, Colorado River, California or Arizona, February 1854, *J. M. Bigelow* (GH; isotypes, NY, PH, US).

DISTRIBUTION: Hillsides and alluvial fans, sometimes in great abundance on sandy slopes, southern Esmeralda County, Nevada, and southwestern Washington County, Utah, south to northern Yuma County, Arizona, and northern Imperial County, California. From ca. 230 ft. below sea level to 6,000 ft. alt.

Camissonia brevipes subsp. *brevipes* grows in more mesic habitats than those occupied by subsp. *arizonica* or subsp. *pallidula*. In the mountains east of Death Valley, for example, *C. claviformis* subsp. *aurantiaca* and *C. brevipes* subsp. *pallidula* are found growing on dry flats, *C. munzii* above in more mesic sites, and *C. brevipes* subsp. *brevipes* in the best watered situations near the tops of the passes. It grows sympatrically with *C. claviformis* subsp. *aurantiaca*, *C. claviformis* subsp. *claviformis*, *C. claviformis* subsp. *funerea*, *C. claviformis* subsp. *integrior*, *C. claviformis* subsp. *peeblesii*, *C. multijuga*, *C. munzii*, and *C. walkeri* subsp. *tortilis*, and forms hybrids with *C. claviformis*, *C. multijuga*, and *C. munzii*. It intergrades with subsp. *pal-*

lidula over a wide area in Utah, Nevada, California, and Arizona, but not with subsp. *arizonica*, with which it does not come in contact. The most densely villous and succulent individuals within subsp. *brevipes* are found in Mohave County, Arizona, and Clark County, Nevada, in the region about Hoover Dam. Progeny of *Everett & Balls* 23034, grown at Claremont, California, were self-incompatible, as were 12 plants from Frenchman Flat, Nye County, Nevada, R18853; 3 from State Hwy. 95, 33.4 miles north of junction with U.S. Hwy. 60–70, San Bernardino County, California, *Kyhos* 65–237; and 3 from 2.9 miles south of Twentynine Palms, San Bernardino County, California, *Kyhos* 64–31. Individuals from the last three populations were tested by pollen-tube growth in selfed and outcrossed individuals. It is surprising that insect visitors to this self-incompatible species appear to be relatively uncommon; nevertheless, full seed set appears to be the rule, except in isolated individuals. Probably a wide spectrum of visitors, active throughout the hours of daylight, is effective in cross-pollinating the plants.

6b. Camissonia brevipes subsp. **pallidula** (Munz) Raven, Brittonia 16: 281. 1964.
Oenothera brevipes var. *pallidula* Munz, Amer. Journ. Bot. 15: 229. 1928.
Oenothera pallidula (Munz) Munz, Leafl. West. Bot. 2: 88. 1938.
Oenothera brevipes subsp. *pallidula* (Munz) Raven, Univ. Calif. Publ. Bot. 34: 83. 1962.

Slender, usually branched above, the stems generally strigose. Terminal leaflet narrowly ovate to ovate. Inflorescence dense, nodding. Hypanthium 4–5 mm. long, yellow within. Sepals strigose, lacking projections, or these poorly developed. Petals 7–12 mm. long, 8–14 mm. wide, often red-dotted near the base. Anthers 4–6 mm. long. Capsule 2–4.2 cm. long; pedicel 2–10 mm. long. Gametic chromosome number, $n=7$. Self-incompatible.

Type: Las Vegas, Clark County, Nevada, 25 April 1905, *M. E. Jones* (POM 38034).

Distribution: Dry flats, often on desert pavement, often with *Larrea* and *Ambrosia dumosa*, from Washington County, Utah, to southeastern Inyo County, California, and south to Riverside County, California, and Mohave County, Arizona, but only along the Colorado River south of Clark County, Nevada. From 250–3,500 ft. alt.

Fourteen plants of this entity from Frenchman Flat, Clark County, Nevada (R18905), were tested for self-compatibility by pollen-tube growth; all were found to be self-incompatible. *Camissonia brevipes* subsp. *pallidula* intergrades with *C. brevipes* subsp. *brevipes* over a wide area, and no evidence for reduction of fertility or for cytological abnormality has been found in the intermediate plants, in spite of the very different phenotypes of these two subspecies (Raven, Univ. Calif. Publ. Bot. 34: 84. 1962). *Camissonia brevipes* subsp. *pallidula*

grows sympatrically with *C. claviformis* subsp. *aurantiaca*, *C. claviformis* subsp. *peeblesii*, *C. munzii*, *C. walkeri* subsp. *tortilis*, and *C. multijuga*, forming natural hybrids with the first two.

6c. Camissonia brevipes subsp. **arizonica** (Raven) Raven, Brittonia 16: 281. 1964.

Oenothera brevipes subsp. *arizonica* Raven, Univ. Calif. Publ. Bot. 34: 84. 1962.

Slender, often branched above, the stems villous. Terminal leaflet narrowly ovate. Inflorescence nodding, the buds individually deflexed before opening. Hypanthium 3–5 mm. long, orange brown within. Sepals villous to strigose, with free caudate portions nearly terminal or lacking. Petals 3–8 mm. long, 4–7 mm. wide, often red-dotted at base, and often fading reddish. Anthers 2.5–5 mm. long. Capsule 1.8–6 cm. long; pedicel 2.5–5 mm. long. Gametic chromosome number, $n=7$.

TYPE: Mohawk Mountains, Yuma County, Arizona, 29 March 1935, *A. & R. A. Nelson* 1343 (RM 172249; isotypes, GH, MO, NY, UC, US).

DISTRIBUTION: Rocky slopes and flats, Yuma County, Arizona, and eastern Imperial County, California. From 250–900 ft. alt.

Plants of *Camissonia brevipes* subsp. *arizonica* from western Arizona are similar to *C. claviformis* subsp. *rubescens*, and the two taxa occur sympatrically in that area. Hybrids between them, however, seem to be rare. The present taxon also grows with *C. claviformis* subsp. *peeblesii* and with *C. claviformis* subsp. *yumae*, forming occasional natural hybrids with each of them.

7. Camissonia multijuga (S. Wats.) Raven, Brittonia 16: 281. 1964.

Oenothera multijuga S. Wats., Amer. Nat. 7: 300. 1873.
Oenothera brevipes var. *parviflora* S. Wats., Amer. Nat. 9: 271. 1875. Type: Valley of the Virgin R., near St. George, Washington Co., Utah, 1874, *C. C. Parry* 74 (GH; isotypes, MO, F); not *Oenothera parviflora* L. 1758.
Chylisma multijuga (S. Wats.) Small, Bull. Torrey Cl. 23: 193. 1896.
Chylisma venosa A. Nels. & Kennedy, Muhlenbergia 3: 140. 1908.
Chylisma hirta A. Nels., Bot. Gaz. 47: 428. 1909. Type: in stony washes, Tuly's Ranch, 13 mi. from Las Vegas, Clark Co., Nevada, 1 May 1905, *L. N. Goodding* 2348 (RM 65187; isotypes, UC, GH, MO).
Chylisma parviflora (S. Wats.) Rydberg, Fl. Rocky Mts. 1064. 1917.
Oenothera brevipes var. *multijuga* (S. Wats.) Jeps., Man. Fl. Pl. Calif. 687. 1925.
Oenothera multijuga var. *typica* Munz, Amer. Journ. Bot. 15: 230. 1928.
Oenothera multijuga var. *parviflora* (S. Wats.) Munz, Amer. Journ. Bot. 15: 231. 1928.
Oenothera watsoni Tidestr., Proc. Biol. Soc. Wash. 48: 41. 1935.
Oenothera phlebophylla Tidestr. Proc. Biol. Soc. Wash. 48: 41. 1935.

Virgate annual or biennial 20–150 cm. tall, with a well-developed basal rosette, nearly leafless above, with numerous divergent branches;

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stems villous, at least below, glabrous or even glaucous above, rarely glandular-pubescent. Basal leaves oblanceolate, villous to nearly glabrous, sometimes purple-dotted, 6–30 cm. long, pinnate or bipinnate, with well-developed narrowly ovate, irregularly serrate lateral leaflets to 2.5 cm. long and 2 cm. wide, alternating with smaller pinnules, the leaflets often divided further; terminal leaflet irregularly serrate, to 6 cm. long and 4 cm. wide, the veins below prominently lined with dark brown oil cells. Inflorescence erect to drooping, sparse, elongating in bud, the buds individually pendulous when mature. Hypanthium 1–3 mm. long, 1–1.5 mm. wide at the summit, glandular-puberulent, villous, or glabrous without, glabrous or villous in lower portions within. Sepals 3–8 mm. long, 1.5–2 mm. wide, glandular-puberulent, strigose, villous, or glabrous, short-caudate at or slightly below the apices. Petals spreading in anthesis, 4–9 mm. long, 4–8 mm. wide, bright yellow, rarely cream, sometimes fading purplish, and of the same color as the stamens, style, and usually the inside of the hypanthium, which may rarely be greenish. Filaments of the episepalous stamens 2.5–4 mm. long, those of the epipetalous ones 1.3–3 mm. long. Anthers 2–4 mm. long, ciliate. Style 7–11 mm. long; stigma 0.7–1 mm. thick, held well above the anthers at maturity. Capsule 1–5.2 cm. long, 1.3–2 mm. thick, slender, straight to slightly curved, glabrous or sparsely villous; pedicel 7–20 mm. long, spreading or rarely slightly deflexed. Seeds 1–1.3 mm. long, 0.8–1 mm. thick. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: Near Kanab, Washington County, Utah, 1872, *Mrs. Ellen P. Thompson* (GH).

DISTRIBUTION: Forming colonies on rocky slopes and banks of eroded sedimentaries, sometimes on gypsum or limestone, often on conglomerates, often with *Pinus edulis* and *Juniperus* or with *Larrea* and *Encelia farinosa*, Washington County, Utah, and southern Lincoln County, Nevada, to northern Mohave County, Arizona. From 1,000–3,500 ft. alt.

Although occupying a relatively limited range, *Camissonia multijuga* is one of the most variable species in its section. Nevertheless, it has not been possible to identify well-marked infraspecific taxa. Plants of *Gullion* 259, 8 miles southwest of Davis Dam, Clark County, Nevada, grown in the experimental garden, were self-incompatible, as were 12 individuals from a population in Eldorado Canyon, Clark County, Nevada, R18970, judging from the comparative growth of pollen tubes in selfed and outcrossed individuals. The autogamous *C. walkeri* subsp. *tortilis* was very probably derived from this entity, and grows sympatrically with it at several localities in southern Nevada, with no direct evidence for hybridization. *Camissonia multi-*

juga also grows sympatrically with *C. brevipes* subsp. *brevipes*, *C. brevipes* subsp. *pallidula*, *C. claviformis* subsp. *aurantiaca*, and *C. parryi*, rarely forming hybrids with both subspecies of *C. brevipes*.

8. Camissonia speculicola (Raven) Raven, Brittonia 16: 282. 1964.

Tufted perennial 10–50 cm. tall, with numerous divergent branches from the base; stems and leaves glabrous or sparsely villous below. Leaves broadly elliptical, 3–20 cm. long, pinnate or often bipinnate, mostly in a basal rosette; lateral leaflets well developed, to 15 mm. long and 7 mm. wide, often further divided and alternating with smaller pinnules; oil cells beneath prominent, dark brown. Inflorescence erect, elongating in flower and fruit, the mature buds individually drooping. Hypanthium 1.5–2 mm. long, 1 mm. across at the summit, glandular-pubescent without, glabrous within. Sepals 2–5 mm. long, 0.5–0.8 mm. wide, glandular-pubescent, caudate with short appendages at the apices, these free in bud. Petals 2–6 mm. long, 1.5–4 mm. wide, bright yellow, fading light purplish, red-dotted near the base, of the same color as inside of hypanthium, stamens, and style; filaments of the episepalous stamens 1.5–3 mm. long, those of the epipetalous ones 1–2 mm. long; anthers 1.2–2 mm. long, glabrous. Style 4–7 mm. long; stigma ca. 0.8 mm. thick, at about the same level as the anthers at anthesis. Capsule straight to slightly curved, spreading to ascending; 0.8–2 cm. long, 1–1.5 mm. thick; glandular-pubescent or glabrous; pedicel 6–10 mm. long; seeds 0.6–1 mm. long, to 0.6 mm. thick. Gametic chromosome number, $n=7$.

Distribution: Washes and debris slides, along the Colorado River in Coconino and Mohave Counties, Arizona, in several disjunct localities. From 2,300–5,600 ft. alt.

8a. Camissonia speculicola subsp. **speculicola**

Oenothera speculicola subsp. *speculicola* Raven, Univ. Calif. Publ. Bot. 34: 87. 1962.

Densely tufted and somewhat woody at base, occasionally with secondary flowering axes arising above from the decumbent stems. Leaves glabrous, glutinous, shining. Style 4–5 mm. long, glabrous. Gametic chromosome number, $n=7$.

Type: Debris slides and crevices in Redwall limestone, Kaibab Trail at 5,400 ft. alt., south rim of Grand Canyon, Coconino County, Arizona, 8 June 1958, *P. H. Raven* 13119 (RSA).

Distribution: Crevices of broken limestone, south rim of the Grand Canyon, Coconino County, Arizona. From 4,500–5,600 ft. alt.

At its type locality, *Camissonia speculicola* subsp. *speculicola* occurs in narrow crevices in the solid limestone, *C. walkeri* subsp. *walkeri* nearby on loose rockslides; no evidence of hybridization between these two entities was noted.

8b. Camissonia speculicola subsp. **hesperia** (Raven) Raven, Brittonia 16: 281. 1964.

Oenothera speculicola subsp. *hesperia* Raven, Univ. Calif. Publ. Bot. 16: 84. 1962.

Less densely tufted and not woody. Leaves sparsely pubescent. Style 5–7 mm. long, pubescent at base.

TYPE: Near Mooney Falls, Havasu Canyon, Coconino County, Arizona, 23 May 1950, *J. T. Howell* 26486 (CAS 359774; isotype, ARIZ).

DISTRIBUTION: Washes and dry stream beds, often on limestone, in two disjunct areas along the Colorado River, Arizona: Havasu and Hualapi Canyons, Coconino County; from Separation Canyon to Spencer Canyon, Mohave County. From 2,300–3,500 ft. alt.

Camissonia speculicola subsp. *hesperia* resembles the allopatric subsp. *speculicola* in its glabrous anthers and distinctive habit. Both of these taxa appear to be outcrossers, but they are probably not self-incompatible, judging from their relatively small flowers (compared with those of the self-incompatible *C. multijuga*). *Camissonia speculicola* subsp. *hesperia* grows sympatrically with *C. walkeri* subsp. *walkeri*.

9. Camissonia walkeri (A. Nels.) Raven, Brittonia 16: 281. 1964.

Slender herb 10–60 cm. tall, villous below and with a basal rosette, the cauline leaves well developed or absent. Basal leaves oblong, with brown oil cells prominently lining veins below, often purple-dotted, doubly serrate, 3–22 cm. long, villous, often densely so below; terminal leaflet 1–5 cm. long, 0.5–3 cm. wide. Inflorescence branching, erect, elongating in flower and fruit, the buds individually drooping. Hypanthium 0.5–1.5 mm. long, glandular-pubescent or hispid without, glabrous to sparsely villous within. Sepals 1.2–4 mm. long, 0.5–1 mm. wide, often purple-dotted, short-caudate at the apices. Petals 1.2–6 mm. long, 0.6–6 mm. wide, bright yellow and of same color as stamens, style, and inside of hypanthium. Filaments of the episepalous stamens 1–3 mm. long, those of the epipetalous ones 0.3–2 mm. long; anthers 0.6–2 mm. long, glabrous or ciliate. Style 1.5–6 mm. long, glabrous or villous at base; stigma ca. 0.6 mm. thick, surrounded by the anthers at maturity. Capsule 1.2–4.5 cm. long, 1.2–1.8 mm. thick, spreading or ascending, the valves often twisted at maturity, straight or slightly curved. Seeds 0.6–1.2 mm. long, 0.4–0.6 mm. thick. Gametic chromosome numbers, $n=7$, 14. Autogamous.

DISTRIBUTION: Washes and alluvial slopes, from Mesa County, Colorado, to southern Elko and Mineral Counties, Nevada, and south to Inyo and northeastern San Bernardino Counties, California; Clark County, Nevada; and Coconino County, Arizona. From ca. 2,000–6,000 ft. alt.

9a. Camissonia walkeri subsp. **tortilis** (Jeps.) Raven, Brittonia 16: 281. 1964.
Oenothera scapoidea var. *tortilis* Jeps., Man. Fl. Pl. Calif. 687. 1925.
Oenothera multijuga var. *parviflora* sensu Munz, Amer. Journ. Bot. 15: 231. 1928, for the most part, excluding the type.
Oenothera walkeri subsp. *tortilis* (Jeps.) Raven, Univ. Calif. Publ. Bot. 34: 90. 1962.

Annual or short-lived perennial, nearly leafless above and with well-developed basal rosette. Leaves pinnate or more rarely bipinnate, the lateral leaflets usually well developed, to 3 cm. long and 1.5 cm. wide, often alternating with smaller pinnules. Hypanthium 1–1.5 mm. long. Sepals 1.5–4 mm. long, often purple-dotted. Petals 2.8–6 mm. long, 2–6 mm. wide. Anthers 1–2 mm. long, glabrous to sparsely ciliate. Style 4–6 mm. long. Capsule on a pedicel 5–30 mm. long. Gametic chromosome number, $n=7$. Autogamous.

Type: Wild Rose Canyon, Panamint Mountains, Inyo County, California, 24 May 1917, *W. L. Jepson* 7131 (JEPS 2669).

Distribution: Colonial in rocky debris near cliffs and along ephemeral streams, often on limestone, Logan (?) and Millard Counties Utah, southern Elko and Mineral Counties, Nevada, and Inyo and northeastern San Bernardino Counties, California, to Clark County, Nevada, and Washington County, Utah. Common only in Inyo County, California. From ca. 2,000–6,000 ft. alt.

Camissonia walkeri subsp. *tortilis* grows sympatrically with *C. brevipes* subsp. *brevipes*, *C. brevipes* subsp. *pallidula*, *C. heterochroma*, and *C. multijuga* without any evidence of hybridization. Although modally very distinct from *C. walkeri* subsp. *walkeri*, subsp. *tortilis* replaces it geographically and their variation patterns overlap to such an extent that I consider it desirable to retain both within the same species.

9b. Camissonia walkeri subsp. **walkeri**
Chylisma walkeri A. Nels., Bot. Gaz. 56: 66. 1913.
Oenothera multijuga var. *orientalis* Munz, Amer. Journ. Bot. 15: 232. 1928. Type: Moab, Grand Co., Utah, 7 June 1913, *M. E. Jones* (POM 38608).
Oenothera walkeri (A. Nels.) Raven, Univ. Calif. Publ. Bot. 34: 88. 1962.

Annual, usually leafy above, the leaves cordate to ovate and simple by reduction of the lateral leaflets, or more rarely these developed; basal rosette not conspicuous. Hypanthium 0.5–1.3 mm. long. Sepals 1.5–2 mm. long. Petals 1.2–3 mm. long, 0.6–1.8 mm. wide. Anthers 0.6–0.8 mm. long, glabrous. Style 1.5–4 mm. long. Capsule on a pedicel 5–15 mm. long. Gametic chromosome numbers, $n=7$, 14. Autogamous.

Type: Dry gypsum hills, Paradox Valley, Montrose County, Colorado, 1 July 1912, *E. P. Walker* 200 (RM 75864; isotypes, DS, GH, POM, US).

Distrubution: Loose slides of limestone and other sedimentaries, or in sandy washes, Mesa County, Colorado, and Emery County,

Utah, south to Montezuma County, Colorado, and central Coconino County, Arizona. From 3,200–5,500 ft. alt.

Under conditions of cultivation, plants of this subspecies develop a rather full rosette of leaves similar to that characteristic of subsp. *tortilis*; in the field, the cauline leaves are very often the only ones present at the time of flowering. Plants of this taxon probably occasionally hybridize with *C. scapoidea* subsp. *scapoidea*; one remarkab'e intermediate population is represented by *Eastwood* 5077 (CAS) from Grand Junction, Mesa County, Colorado, with the pubescence and cauline leaves of *C. walkeri* subsp. *walkeri* but the habit of *C. scapoidea* subsp. *scapoidea*. *Camissonia walkeri* subsp. *walkeri* grows sympatrically with both subspecies of *C. speculicola* but in less stable soil and without any evidence of hybridization. *Camissonia scapoidea* subsp. *scapoidea*, on the other hand, is mostly restricted to alkaline clay flats and is thus usually ecologically separated from *C. walkeri* subsp. *walkeri*.

An apparent autotetraploid population of *C. walkeri* subsp. *walkeri* has been found growing on the walls of the Marble Gorge, Coconino County, Arizona. These plants had up to 4 rings of 4 chromosomes at meiotic metaphase I (Raven, Univ. Calif. Publ. Bot. 34: 40. 1962). Seven other individuals from four other populations were diploid.

10. Camissonia claviformis (Torr. & Frém.) Raven, Brittonia 16: 282. 1964.

Annual 3–70 cm. tall, branching mostly from the base. Leaves in a prominent basal rosette, reduced upward, pinnately divided or entire by reduction, 1.5–20 cm. long, broadly oblanceolate, the terminal segment 0.8–9 cm. long, 0.2–4 cm. broad, lanceolate to cordate, the lateral segments lacking or to 2.5 cm. long; veins beneath prominently lined with brown oil cells. Inflorescence nodding, not elongating much in flower. Flowers opening in late afternoon in all except subsp. *cruciformis*. Hypanthium 1.5–6.5 mm. long, 1–5 mm. across at the summit, short-villous in lower portions within. Sepals 2–8 mm. long, 1–2.5 mm. wide, with brown oil cells on midribs above and on free tips, if present. Petals 1.5–8 mm. long, 1.5–10 mm. wide, yellow or white, reflexed in anthesis, and of same color as stamens and style. Stamens subequal, the filaments 1.5–5.5 mm. long, dilated at base; anthers 1.5–6 mm. long, long-ciliate. Style 5–16 mm. long, held well above the stamens at anthesis; stigma greenish, 0.6–1.3 mm. thick. Capsule 0.9–3.8 cm. long, 1.5–2.3 mm. thick, straight or curved, clavate, on a spreading or ascending pedicel 4–40 mm. long. Seeds pale brown, narrowly obovoid, lenticular, 0.6–1.5 mm. long. Gametic chromosome number, $n=7$. Self-incompatible.

DISTRIBUTION: Sandy slopes and flats, often in washes, from southeastern Oregon and adjacent Idaho south to eastern California,

Nevada, and Arizona, northwestern Sonora, and to near latitude 29° N. in eastern Baja California. From ca. 250 ft. below sea level to 6,500 ft. alt.

Camissonia claviformis is the most complex and one of the most widely distributed species of the genus. The central part of its range is occupied by five closely related white-flowered subspecies, *claviformis*, *aurantiaca*, *funerea*, *integrior*, and *peeblesii*, so similar morphologically that they could be regarded as a single taxon. South of this area are found four additional subspecies, all yellow-flowered, namely, *peirsonii*, *rubescens*, *wigginsii*, and *yumae*. These entities have sepals and flower color similar to those of *C. brevipes*, and it is likely that they were derived following hybridization between that species and white-flowered populations of *C. claviformis*. North of the range of the white-flowered subspecies are found two additional yellow-flowered subspecies, *cruciformis* and *lancifolia*, the latter apparently derived following hybridization between the former and some of the white-flowered subspecies. Most populations of subsp. *cruciformis* consist of plants in which the flowers open in the early morning; all other subspecies consist of plants that have flowers opening in the late afternoon. In this and other morphological respects, *C. claviformis* subsp. *cruciformis* (including subsp. *citrina*) resembles *C. eastwoodiae* and *C. munzii* and is undoubtedly close to the ancestral stock from which *C. claviformis* was derived.

10a. Camissonia claviformis subsp. **cruciformis** (Kell.) Raven, Brittonia 16: 282. 1964.

Oenothera cruciformis Kell., Proc. Calif. Acad. Sci. 2: 227, *fig. 71.* 1873.

Chylisma clavaeformis var. *cruciformis* (Kell.) Small, Bull. Torrey Cl. 23: 193. 1896.

Chylisma cruciformis (Kell.) Howell, Fl. N. W. Amer. 233. 1898.

Oenothera clavaeformis var. *cruciformis* (Kell.) Munz, Amer. Journ. Bot. 15: 235. 1928.

Oenothera clavaeformis var. *purpurascens* sensu Munz, Leafl. West. Bot. 3: 53. 1941; not S. Wats. 1873.

Oenothera clavaeformis subsp. *cruciformis* (Kell.) Raven, Univ. Calif. Publ. Bot. 34: 108. 1962.

Oenothera clavaeformis subsp. *citrina* Raven, Univ. Calif. Publ. Bot. 34: 108. 1962. Type: Roadbanks of decomposed conglomerate, in clay soil, 1.4 mi. NE. of Oregon State line on U.S. Hwy. 95, Jump Creek Canyon, Owyhee Co., Idaho, 23 June 1958, *P. H. Raven & O. T. Solbrig* 13385A (RSA).

Plants 3–55 cm. tall, strigose or glandular below and often glandular above, or glabrous. Lateral leaflets few to numerous; terminal leaflet to 8 cm. long and to 4 cm. wide, narrowly ovate to nearly cordate, serrate with scattered teeth. Flowers usually opening near sunrise. Hypanthium 2–6.5 mm. long, sparsely strigose or glandular without, yellow or orange brown within. Sepals sparsely strigose or glandular-pubescent. Petals 2.5–8 mm. long, 2.5–10 mm. wide, bright yellow,

often red-dotted at the base and often fading purple. Filaments 2–5 mm. long; anthers 2–6 mm. long. Style 7–16 mm. long. Capsule 0.8–2.8 cm. long, glandular-pubescent to glabrous, pedicel 4–30 mm. long. Gametic chromosome number, $n=7$. Self-incompatible.

NEOTYPE: Steamboat Springs, Washoe County, Nevada, 28 May 1959, *P. H. Raven* 14269 (RSA). The type specimen, if one was prepared, has not been preserved; the proposed neotype is from the type locality and a close match for Proc. Calif. Acad. Sci. 2, *fig. 71* (p. 228). See Raven, Univ. Calif. Publ. Bot. 34: 108. 1962.

DISTRIBUTION: Sandy or clayey flats and slopes, with *Artemisia tridentata*, *Purshia tridentata*, *Grayia spinosa*, or *Chrysothamnus*, Lake, Harney, and Malheur Counties, Oregon, western Canyon and Owyhee Counties, Idaho, central and southern Washoe County, Nevada, and Lassen County, California. From 2,000–4,600 ft. alt.

Camissonia claviformis subsp. *cruciformis* is unusually variable, probably owing to hybridization between its southern populations (which occupy a disjunct area) and subsp. *integrior*, which they contact locally. The populations of this taxon found in the vicinity of Sparks, Washoe County, Nevada, consist of plants that have flowers opening in the evening; all other populations of the subspecies appear to have flowers opening in the morning, near sunrise. This taxon intergrades with *C. claviformis* subsp. *integrior* and occurs sympatrically with *C. scapoidea* subsp. *brachycarpa*.

Four populations of this subspecies were tested for pollen-tube growth following self- and cross-pollination and found to be self-incompatible: 4.5 miles north of Sparks, Washoe County, Nevada (8 plants); Steamboat Springs, Washoe County, Nevada (15 plants); 4.2 miles west of Rome, Malheur County, Oregon (3 plants, *Kyhos* 65–255); Jump Creek Canyon, Owyhee County, Idaho (13 plants).

10b. Camissonia claviformis subsp. **lancifolia** (Heller) Raven, Brittonia 16: 282. 1964.

Chylismia lancifolia Heller, Muhlenbergia 2: 226. 1906.

Oenothera clavaeformis var. *cruciformis* sensu Munz, Amer. Journ. Bot. 15: 235. 1928.

Oenothera clavaeformis subsp. *lancifolia* (Heller) Raven, Univ. Calif. Publ. Bot. 34: 109. 1962.

Plants 5–60 cm. tall, strigose below, glabrous and often glaucous above; rosette not strictly basal, the leaves erect. Lateral leaflets few or wanting; terminal leaflet to 5 cm. long and 2.8 cm. wide, lanceolate, the apex acuminate, unevenly serrate, the serrations tipped with light brown clusters of oil cells. Hypanthium 3.5–6 mm. long, glabrous without and orange brown within. Sepals glabrous or sparsely strigose near the apices. Petals 3.5–7 mm. long, 4–9 mm. wide, bright yellow, usually red-dotted near the base. Filaments 3–5 mm. long; anthers

3.5–5 mm. long. Style 9–16 mm. long. Capsule 1.1–2.8 cm. long, glabrous or nearly so; pedicel 8–18 mm. long, Gametic chromosome number, $n=7$.

TYPE: Base of the White Mountains east of Laws, Inyo County, California, 11 May 1906, *A. A. Heller* 8231 (US 611229; isotypes, CAS, COLO, DS, MO, UC).

DISTRIBUTION: Sandy slopes and flats, often with *Artemisia tridentata* or *Chrysothamnus*, east of the Sierra Nevada in southern Mono and Inyo Counties, California. From 4,000–5,500 ft. alt.

The southernmost station for *C. claviformis* subsp. *lancifolia*, in the Owens Valley, Inyo County, California, 3 miles north of Big Pine, is approximately 24 miles north of the northernmost for subsp. *claviformis*, 7.7 miles north of Independence. The yellow-flowered subspecies reaches its peak of bloom several weeks later than the white-flowered one. *Camissonia claviformis* subsp. *lancifolia* grows sympatrically with *C. heterochroma*.

10c. Camissonia claviformis subsp. **integrior** (Raven) Raven, Brittonia 16: 282. 1964.

Oenothera scapoidea var. *purpurascens* S. Wats., Proc. Amer. Acad. 8: 595. 1873. Lectotype: Not abundant, islands in Mono L., Mono Co., California, 10–11 July 1863, *W. H. Brewer* 1845 (GH; isotypes, UC, US).

Oenothera clavaeformis var. *typica* sensu Munz, Amer. Journ. Bot. 15: 236. 1928.

Oenothera clavaeformis subsp. *integrior* Raven, Univ. Calif. Publ. Bot. 34: 106. 1962.

Plants 6–70 cm. tall, strigose below and usually glandular-pubescent above, the leaves sometimes purple-dotted. Lateral leaflets few or absent; terminal leaflet to 7 cm. long and 3 cm. wide, narrowly ovate to ovate, often subcordate at the base, serrate, the serrations often tipped with clusters of oil cells. Hypanthium 3–6 mm. long, strigose, glandular, or nearly glabrous without, orange brown within. Sepals rarely purple-dotted, strigose, glandular, or nearly glabrous, rarely with short free caudate portions. Petals 4.5–8 mm. long, 4–10 mm. wide, occasionally purple-dotted at base, fading purple. Filaments 3–5.5 mm. long. Anthers 3–5.5 mm. long. Style 10–16 mm. long. Capsule 13–25 mm. long, glabrous, strigose, or glandular; pedicel 15–40 mm. long. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: Palisade, Eureka County, Nevada, 14 June 1882, *M. E. Jones* 3869 (POM 38505; isotypes, CAS, DS, MO, NY, UC, US, UTC).

DISTRIBUTION: Dry flats in Great Basin desert, with *Artemisia tridentata*, *Chrysothamnus*, or *Juniperus*, often forming large colonies on banks and flats, from southern Harney County, Oregon, southward nearly throughout Nevada to Lincoln and Esmeralda Counties and to

Mono and northeastern Inyo Counties, California. From 4,000–6,500 ft. alt.

This is the most widely distributed subspecies of *C. claviformis*, and is markedly variable in kind and amount of pubescence. It intergrades with subsp. *aurantiaca* and with subsp. *cruciformis* and grows sympatrically with *C. brevipes* subsp. *brevipes* (forming occasional hybrids), *C. heterochroma* and *C. scapoidea* subsp. *brachycarpa*. Three populations from Nevada were sampled for self-compatibility, and 15 plants from 20 miles northeast of Lovelock, Pershing County (R18542), 9 from Palisade, Eureka County, and 20 from 28.9 miles southwest of Lovelock, Churchill County (*Kyhos* 65–254) were found to be self-incompatible by pollen-tube growth.

10d. Camissonia claviformis subsp. **funerea** (Raven) Raven, Brittonia 16: 282. 1964.

Oenothera clavaeformis var. *aurantiaca* sensu Munz, Amer. Journ. Bot. 15: 237. 1928; pro parte.

Oenothera clavaeformis subsp. *funerea* Raven, Univ. Calif. Publ. Bot. 34: 106. 1962.

Plants 6–60 cm. tall, strigose below, often densely so. Lateral leaflets well developed or more often wanting; terminal leaflet to 8 cm. long and to 4.5 cm. wide, ovate, often cordate at the base, very prominent, dentate. Hypanthium 3–5.5 mm. long, strigose without, usually densely so, orange brown within. Sepals usually densely strigose, with conspicuous free caudate segments arising on midribs just below apices. Petals 3.5–7.5 mm. long, 3.5–7.5 mm. wide, often fading purple. Filaments 3–5.5 mm. long; anthers 3–4.5 mm. long. Style 8–12 mm. long, Capsule 1.2–3.2 cm. long, strigose; pedicel 8–22 mm. long. Gametic chromosome number, $n=7$.

TYPE: Dry wash, 2 miles east of Stovepipe Wells, Death Valley, Inyo County, California, 7 April 1928, *P. A. Munz & C. L. Hitchcock* 11030 (POM 159488; isotypes, GH, UC, US).

DISTRIBUTION: Dry slopes and flats, with *Larrea* and *Ambrosia dumosa*, Eureka Valley, Saline Valley, and the region of Death Valley, Inyo County, and northernmost San Bernardino County, California. From ca. 250 ft. below sea level to 3,000 ft. alt.

This taxon is geographically coherent and distinct in its more extreme forms, but intergrades with subsp. *aurantiaca* and subsp. *claviformis* over a broad front, producing an array of intermediate forms. It occurs sympatrically with *C. munzii* and with *C. brevipes* subsp. *brevipes*, forming occasional hybrids with each of these species.

10e. Camissonia claviformis subsp. **claviformis**

Oenothera clavaeformis Torr. & Frém., Rep. Expl. Exped. Rocky Mts. 314. 1845.

Oenothera scapoidea var. *clavaeformis* (Torr. & Frém.) S. Wats., Bot. King Expl. 109. 1871.

Chylisma scapoidea var. *clavaeformis* (Torr. & Frém.) Small, Bull. Torrey Cl. 23: 194. 1896.
Chylisma clavaeformis (Torr. & Frém.) Heller, Muhlenbergia 2: 105. 1906.
Oenothera clavaeformis var. *typica* Munz, Amer. Journ. Bot. 15: 236. 1928.
Chylismia clavaeformis var. *typica* (Munz) Johansen, Amer. Journ. Bot. 16: 597. 1929.
Oenothera clavaeformis subsp. *clavaeformis* Raven, Univ. Calif. Publ. Bot. 34: 99. 1962.

Plants 6–55 cm. tall, glabrous or strigose below and occasionally glandular, the leaves sometimes purple-dotted. Lateral leaflets usually well developed; terminal leaflet to 6 cm. long and 3.5 cm. wide, narrowly ovate, irregularly sinuate-dentate. Hypanthium 3–5.5 mm. long, glabrous, sparsely strigose, or rarely glandular without, orange brown within. Sepals glabrous, sparsely strigose, or rarely glandular, with short-caudate terminal portions. Petals 3.5–8 mm. long, 4–8 mm. wide, white, very rarely pale yellow, sometimes purple-dotted at base, often fading purple. Filaments 3–5 mm. long; anthers 3–4 mm. long. Style 8–12 mm. long. Capsule 1.2–3 cm. long, glabrous or sparsely pubescent; pedicel 10–25 mm. long. Gametic chromosome number, $n = 7$. Self-incompatible.

Type: Frémont's 2d Expedition (NY). Collected in 1844 by J. C. Frémont. The herbarium specimen selected as the lectotype by Munz (Amer. Journ. Bot. 15: 236. 1928) and cited by him as "Fremont's Pac. R. R. Exp., 1843–'44, 'probably collected in California,' " has not been located, but this may be an erroneous citation of a specimen from the Torrey Herbarium (NY) labeled "Fremont's Pacific R. Road Expedition, 1853–54 (Probably collected in California)." This collection might be an isotype, but if so it is incorrectly labeled.

Distribution: Alluvial slopes and flats, with *Larrea* and *Ambrosia dumosa*, western Inyo County, eastern Kern County, northern Los Angeles County, western San Bernardino County, and northern Riverside County, California, almost entirely on the Mojave Desert. From 2,800–5,500 ft. alt.

This subspecies intergrades gradually and throughout a broad area with subsp. *aurantiaca* and with subsp. *funerea*. It occurs sympatrically with *C. brevipes* subsp. *brevipes*, forming occasional hybrids with this entity. Isolated plants of this subspecies fail to set fruit, and more direct evidence of its self-incompatibility was provided by a study of pollen-tube growth following self- and cross-pollination in three plants from each of the following localities in California: near Pearblossom, Los Angeles County, *Kyhos* 64–14; Joshua Tree, San Bernardino County, *Kyhos* 64–33.

10f. Camissonia claviformis subsp. **aurantiaca** (S. Wats.) Raven, Brittonia 16: 282. 1964.
Oenothera scapoidea var. *aurantiaca* S. Wats., Proc. Amer. Acad. 8: 595. 1873.
Chylismia scapoidea var. *aurantiaca* (S. Wats.) A. Davids. & Moxley, Fl. S. Calif. 254. 1923.

Oenothera clavaeformis var. *aurantiaca* (S. Wats.) Munz, Amer. Journ. Bot. 15: 237. 1928.
Chylismia aurantiaca (S. Wats.) Johansen, Desert 3: 78. 1931.
Oenothera clavaeformis subsp. *aurantiaca* (S. Wats.) Raven, Univ. Calif. Publ. Bot. 34: 100. 1962.

Plants 5–50 cm. tall, strigose, especially below, and rarely glandular-pubescent above, the leaves sometimes purple-dotted. Lateral leaflets up to 25 on each side of rachis, irregular, and well developed; terminal leaflet to 3 cm. long and 1.5 cm. wide, narrowly ovate, irregularly sinuate-dentate. Hypanthium 3–5 mm. long, strigose without, orange brown within. Sepals strigose, rarely with short free caudate tips in bud. Petals 2.5–8 mm. long, 3.5–8 mm. wide, white, rarely purple-dotted at base, often fading purple, rarely orange. Filaments 2–5 mm. long; anthers 2.5–4.5 mm. long. Style 7.5–14 mm. long. Capsule 1.3–3 cm. long, sparsely strigose or glabrous; pedicel 8–25 mm. long. Gametic chromosome number, $n=7$. Self-incompatible.

LECTOTYPE: Fort Mohave, Mohave County, Arizona, 1861, *J. G. Cooper* (GH; isotypes, UC, US); Munz, Amer. Journ. Bot. 15: 237. 1928.

DISTRIBUTION: Common on sandy flats and washes, with *Larrea*, *Ambrosia dumosa*, and *Fouquieria splendens*, from Lincoln County, Nevada, south to northeasternmost Baja California, and in Arizona only in westernmost Mohave and Yuma Counties. From 230 ft. below sea level to 3,000 ft. alt.

Camissonia claviformis subsp. *aurantiaca* is variable in leaf outline and color and in amount of pubescence. It intergrades completely with the other four white-flowered subspecies, *claviformis*, *funerea*, *integrior*, and *pebblesii*. It likewise intergrades with subsp. *yumae* and subsp. *peirsonii* where it comes in contact with them. Occasional plants have large amounts of glandular pubescence in the inflorescence and elsewhere, as subsp. *peeblesii*, but nowhere west of the Colorado River do such individuals exceed 50 percent of any population known to me. *Camissonia claviformis* subsp. *aurantiaca* grows sympatrically with *C. brevipes* subsp. *brevipes*, *C. brevipes* subsp. *pallidula*, *C. multijuga*, and *C. munzii*, forming occasional hybrids with the first two and last entities. Three individuals each from two populations of this subspecies from California were shown to be self-incompatible by pollen-tube growth in selfed and outcrossed flowers: 0.7 mile from U.S. Hwy. 99 on road to Snow Creek, Riverside County, *Kyhos* 64–3; 4.3 miles south of Mortmar, Imperial County, *Kyhos* 64–13.

10g. Camissonia claviformis subsp. **peeblesii** (Munz) Raven, Brittonia 16: 282. 1964.
Oenothera clavaeformis var. *aurantiaca* sensu Munz, Amer. Journ. Bot. 15: 237. 1928.
Oenothera clavaeformis var. *peeblesii* Munz, Leafl. West. Bot. 2: 158. 1939.

Camissonia clavaeformis subsp. *peeblesii* (Munz) Raven, Univ. Calif. Publ. Bot. 34: 101. 1962.

Plants 5–60 cm. tall, glandular-pubescent, especially above, and often also strigose below. Leaves glandular-pubescent, the lateral leaflets numerous, irregular, and well developed, the terminal leaflet narrowly ovate, irregularly sinuate-dentate, to 7 cm. long and 3 cm. wide. Hypanthium 3–5.5 mm. long, glandular-pubescent or strigose without, orange brown within. Sepals glandular-pubescent, strigose, or both, usually lacking caudate appendage. Petals 3–7.5 mm. long, 3–5 mm. wide, often fading purple. Filaments 2–3 mm. long; anthers 2.5–4 mm. long. Style 7.5–14 mm. long. Capsule 1.5–3 cm. long, glandular-pubescent or strigose; pedicel 4–32 mm. long. Gametic chromosome number, $n=7$.

TYPE: Casa Grande, Pinal County, Arizona, 25 February 1927, *Peebles & Harrison* 3537 (US 1367424; isotype, ARIZ).

DISTRIBUTION: Flat sandy plains and washes, with *Prosopis*, *Carnegiea gigantea*, *Larrea* and *Ambrosia dumosa*, throughout almost all the southwestern half of Arizona and locally in northwesternmost Sonora. From 400–2,000 ft. alt.

I have included in *Camissonia claviformis* subsp. *peeblesii* all populations in which a majority of the plants have some glandular pubescence, and the resulting taxon has a coherent geographical range. It intergrades completely with subsp. *aurantiaca* and with subsp. *rubescens*, growing in part in the same area as the latter. It also occurs sympatrically with all three subspecies of *C. brevipes*, forming occasional hybrids with them.

10h. Camissonia claviformis subsp. **peirsonii** (Munz) Raven, Brittonia 16: 282. 1964.

Oenothera clavaeformis var. *peirsonii* Munz, Amer. Journ. Bot. 15: 238. 1928.
Chylismia peirsonii (Munz) Johansen (as "piersonii"), Desert 3: 78. 1931.
Oenothera clavaeformis subsp. *peirsonii* (Munz) Raven, Univ. Calif. Publ. Bot. 34: 105. 1962.

Plants 5–60 cm. tall, spreading-villous below and often above, more rarely strigose or with glandular pubescence. Lateral leaflets usually well developed; terminal leaflets to 9 cm. long and to 3.5 cm. wide, narrowly ovate, irregularly sinuate-dentate. Hypanthium 2.5–4.5 mm. long, villous or strigose without, orange brown within. Sepals villous or strigose, with conspicuous free caudate segments arising just below apices of midribs. Petals 4.5–7 mm. long, 4–9 mm. wide, yellow, more rarely white, not changing color in fading. Filaments 3.5–5 mm. long; anthers 3.5–5 mm. long. Style 9–14 mm. long. Capsule 1.2–3.8 cm. long, spreading pubescent (rarely glabrous); pedicel 10–20 mm. long. Gametic chromosome number, $n=7$.

TYPE: Twenty-eight miles south of Coachella, Imperial County, California, 12 April 1922, *F. W. Peirson* 4512 (POM 138409; isotype, RSA).

DISTRIBUTION: Sandy fields and washes, with *Larrea, Ambrosia dumosa,* and *Fouquieria splendens,* east of the Salton Sea and Imperial Valley in San Diego and Imperial Counties, California, and in northeastern Baja California to the Gulf of California. From 240 ft. below sea level to 1,000 ft. alt.

This subspecies intergrades with subsp. *aurantiaca* in northeastern San Diego County, California, where it is extremely variable in pubescence, leaf color, and flower color. Since publishing my revision of the group, I have seen a specimen of *C. claviformis* subsp. *peirsonii* from 41 miles south of San Felipe, Baja California, *Wiggins* 18162 (DS), this record establishing a new southern limit for the subspecies. One additional determination of chromosome number has been made in this entity, $n=7$, in *Klein* 1175 (RSA), from 2 miles south of San Felipe, Baja California.

10i. Camissonia claviformis subsp. **yumae** (Raven) Raven, Brittonia 16: 282. 1964.
Oenothera clavaeformis subsp. *yumae* Raven, Univ. Calif. Publ. Bot. 34: 104. 1962.

Plants 5–40 cm. tall, strigose pubescent below, often densely, and sometimes glandular-pubescent above. Lateral leaflets well developed or reduced; terminal leaflet to 6.5 cm. long and to 2 cm. wide, lanceolate, irregularly sinuate-dentate. Hypanthium 2.5–4 mm. long, strigose without, orange brown within. Sepals strigose with short free caudate portions arising just below the apices, or these absent. Petals 3–5 mm. long, 4–5.5 mm. wide, pale yellow, fading reddish or not changing color after pollination. Filaments 2–4 mm. long, anthers 2–4 mm. long. Style 7.5–10 mm. long. Capsule 1.2–3.2 cm. long, strigose; pedicel 5–30 mm. long. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: Covering dunes, Yuma Desert 4.8 miles west of summit of Telegraph Pass, Yuma County, Arizona, 28 February 1958, *P. H. Raven* 11724 (RSA).

DISTRIBUTION: Very dry dunes and sandy flats with *Larrea* and *Ambrosia dumosa,* southeastern Imperial County, California, Yuma Desert, Arizona, and from El Gran Desierto to Puerto Peñasco in northwestern Sonora, and in northeastern Baja California (8 miles northwest of La Ventana, *Moran* 12354, DS, SD). From sea level to 300 ft. alt.

This subspecies, which is unusually variable, was almost certainly derived following hybridization between the yellow-flowered subsp. *peirsonii* and the white-flowered subsp. *aurantiaca*. It intergrades with subsp. *aurantiaca* in California and Baja California and with subsp. *peeblesii* in Arizona and Sonora. It grows sympatrically with *C. brevipes* subsp. *arizonica*, but no hybrids have been found. Three individuals from a population along U.S. Hwy. 80,

0.4 mile west of the junction with U.S. Hwy. 98, Imperial County, California, *Kyhos* 64–11, were found to be self-incompatible, judging from pollen-tube growth in self-pollinated flowers.

10j. Camissonia claviformis subsp. **wigginsii** (Raven) Raven, Brittonia 16: 282. 1964.

Oenothera clavaeformis subsp. *wigginsii* Raven, Univ. Calif. Publ. Bot. 34: 103. 1962.

Plants 5–20 cm. tall, covered with spreading white trichomes below and glandular pubescence above. Lateral leaflets reduced or absent; terminal leaflet to 3 cm. long and to 1.5 cm. wide, narrowly ovate, irregularly sinuate-dentate. Hypanthium 1.5–2 mm. long, villous and often purple-dotted without, orange brown within. Sepals villous, often purple-dotted, with short free caudate portions arising on midribs below the apices. Petals 1.5–2 mm. long, 1.5–2 mm. wide, yellow, fading brick red after pollination. Filaments 1.5–2 mm long; anthers 1.5–2 mm. long. Style 5–7 mm. long. Capsule (1.5–) 2.5–3.5 cm. long, often purple-dotted, villous; pedicel 8–20 mm. long. Gametic chromosome number, $n=7$.

TYPE: Wash 3 miles from Los Angeles Bay, Baja California, Mexico, 20 February 1935, *I. L. Wiggins* 7684 (DS 265606; isotypes F, GH, UC, US).

DISTRIBUTION: Central Baja California, in washes. From ca. 500–ca. 2,000 ft. alt.

This is apparently a rare and rather restricted subspecies most similar to subsp. *peirsonii* and subsp. *rubescens*, from which it differs principally in flower size. It is, however, separated from the former subspecies, the nearest geographically within the species, by a gap of about 75 miles. In spite of its relatively small flowers, the stigma is held well above the anthers and this subspecies is presumably self-incompatible like the rest of the species. The chromosome number was determined in a collection from the Arroyo San Francisquito 5 miles northwest of Las Arrastras, 29°37′ N. lat., 114°27′ W. long., *Moran* 12402 (DS, SD).

10k. Camissonia claviformis subsp. **rubescens** (Raven) Raven, Brittonia 16: 282. 1964.

Oenothera clavaeformis subsp. *rubescens* Raven, Univ. Calif. Publ. Bot. 34: 103. 1962.

Plants 5–40 cm. tall, covered, especially below, with spreading white trichomes, and also with short glandular trichomes. Lateral leaflets few or absent; terminal leaflet to 4 cm. long and 2 cm. wide, lanceolate, irregularly dentate. Hypanthium 3.5–5 mm. long, glandular-pubescent or villous or both, orange brown within. Sepals villous or glandular-pubescent, with conspicuous free caudate segments arising from midribs below the apices. Petals 3–5 mm. long, 3–5 mm. wide, yellow, fading brick red after pollination. Filaments 2.5–5

mm. long; anthers 2.5–4 mm. long. Style 7–12 mm. long. Gametic chromosome number, $n=7$.

TYPE: On sandy flats, 24 miles south of Sonoyta on road to Rocky Point (Punta Peñasco), Distrito de Altar, Sonora, 14 March 1936, *D. D. Keck* 4178 (DS 287997; isotypes, GH, POM, UC, US).

DISTRIBUTION: Sandy flats, with *Larrea*, *Ambrosia dumosa*, and *Carnegiea gigantea*, western Maricopa, eastern Pima, and southeastern Yuma Counties, Arizona, and northwestern Sonora. From 200–1,000 ft. alt.

This entity grows sympatrically with *C. brevipes* subsp. *arizonica* and occasionally forms natural hybrids with it. It intergrades with *C. claviformis* subsp. *peeblesii*.

11. Camissonia munzii (Raven) Raven, Brittonia 16: 281. 1964.
Oenothera munzii Raven, Univ. Calif. Publ. Bot. 34: 91. 1962.

Annual herb 8–50 cm. tall, with numerous branches at the base and above, the leaves mostly in a subbasal rosette. Stems and leaves strigose, often densely so above and in the inflorescence. Leaves to 20 cm. long, pinnate, with well-developed lateral leaflets; terminal leaflet ovate, to 6 cm. long and 3 cm. wide, the veins lined below with brownish oil cells. Inflorescence nodding, not congested, elongating in mature bud. Hypanthium 2–3 mm. long, 2–3 mm. across at the summit, strigose without, villous and orange brown within. Sepals 4–7 mm. long, 1.5–2 mm. wide, strigose. Petals 3–10 mm. long, 3–10 mm. wide, bright yellow, red-dotted near the base. Stamens subequal, the filaments 4–8 mm. long; anthers 3–6 mm. long, ciliate. Style 8–18 mm. long; stigma 0.6–0.8 mm. thick, held well above the anthers at anthesis. Capsule 0.8–2.4 cm. long, 1.5–2 mm. thick, clavate; pedicel 8–28 mm. long, widely divergent and becoming sharply deflexed at maturity. Seeds pale brown, 0.8–1.6 mm. long, 0.5–0.8 mm. thick. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: Sandy desert wash, Salsberry Pass, south end of Death Valley, Inyo County, California, 9 April 1940, *P. A. Munz* 16474 (POM 255191; isotypes, CAS, GH, NA, POM, RSA, UC, US, WS, WTU).

DISTRIBUTION: Relatively mesic slopes and washes at middle elevations in the mountains at the north end, eastward, and south of Death Valley, from Saline Valley and the Grapevine Mountains, Inyo County, California, and Yucca Flat, Nye County, Nevada, southward to the Kingston Range, San Bernardino County, California. From 2,000–5,000 ft. alt.

Camissonia munzii grows sympatrically with *C. brevipes* subsp. *brevipes*, *C. brevipes* subsp. *pallidula*, *C. claviformis* subsp. *funerea*, *C. claviformis* subsp. *aurantiaca*, and *C. heterochroma*, forming occasional hybrids with the first and fourth mentioned taxa. It is readily dis-

tinguished by its long, deflexed pedicels and clavate capsules. A population from 7.2 miles south of Mercury, Nye County, Nevada, R18865, was tested for self-compatibility, and 14 individuals were found to be self-incompatible by pollen-tube growth.

12. Camissonia eastwoodiae (Munz) Raven, Brittonia 16: 282. 1964.

Oenothera scapoidea var. *eastwoodae* Munz, Amer. Journ. Bot. 15: 234. 1928.

Oenothera eastwoodiae (Munz) Raven, Univ. Calif. Publ. Bot. 34: 92. 1962.

Succulent annual 3–30 cm. tall, the stems glabrous, glandular-pubescent, or villous below. Leaves mostly basal, entire or sparsely denticulate, simple, the blades oblanceolate to cordate, darker green above, 0.8–7.5 cm. long, 0.4–3 cm. wide; veins below lined with pale brown oil cells; petioles 0.5–8 cm. long. Inflorescence drooping, elongating in flower and fruit. Hypanthium 2–4.5 mm. long, 1.5–3.4 mm. across at the summit, glandular-pubescent or strigose without, villous in lower portions within. Sepals 3–8 mm. long, 1–2.5 mm. wide, glandular-pubescent, strigose, or glabrous, without caudate appendage. Petals 5.5–9 mm. long, 4–10 mm. wide, bright yellow and of same color as stamens, style, and inside of hypanthium, red-dotted near the base. Filaments of the episepalous stamens 3–8 mm. long, those of the epipetalous ones 2.8–5.5 mm. long; anthers 2–4 mm. long, ciliate. Style 10–17 mm. long; stigma 0.6–0.8 mm. thick, held well above the stamens at anthesis, villous near the base. Capsule 1.8–4 cm. long, curved, erect, on a spreading or slightly deflexed pedicel 4–28 mm. long. Seeds tan, 1.2–1.7 mm. long. Gametic chromosome number, $n=7$.

TYPE: Grand Junction, Mesa County, Colorado, May 1892, *A. Eastwood* (GH; isotypes, UC, US).

DISTRIBUTION: Clay flats, on gray alkaline marine-deposited gumbo, and in sandy draws, Mesa County, Colorado, and Emery County, Utah, south to San Juan County, Utah. From 4,000–5,500 ft. alt.

Camissonia eastwoodiae, the only outcrossing species in the eastern part of the range of sect. *Chylismia*, is undoubtedly self-incompatible. It grows sympatrically with the autogamous *C. scapoidea* subsp. *scapoidea* and in the same vicinity as the ecologically distinct *C. walkeri* subsp. *walkeri*.

13. Camissonia scapoidea (Torr. & Gray) Raven, Brittonia 16: 95. 1964.

Annual 3–45 cm. tall; stems strigose, villous, or glandular-pubescent below. Leaves mostly in a basal rosette, greatly reduced upward, spatulate, 1–18 cm. long, the lateral leaflets well developed or absent. Inflorescence drooping, glandular-pubescent, strigose, or nearly glabrous. Hypanthium 1–4 mm. long, 1–3.5 mm. across at the summit, glandular-pubescent, strigose, or glabrous without, sparsely villous to glabrous within. Sepals 1.2–5 mm. long, 1–2 mm. wide, strigose,

glandular-pubescent, or glabrous, entire or short-caudate at the apices. Petals 1.5–5.5 mm. long, 1–4 mm. wide, bright yellow, of same color as stamens, style, and inside of hypanthium. Filaments of the episepalous stamens 1.2–6 mm. long, those of the epipetalous ones 0.5–4 mm.; anthers 1–2.5 mm. long, ciliate or glabrous. Style glabrous or short-villous at the base, 3–11 mm. long; stigma 0.3–0.6 mm. thick, surrounded by anthers, at least the longer ones, at anthesis. Capsule ascending, curved to nearly straight, 0.8–4 cm. long, 1.8–2.6 mm. thick, sparsely pubescent to glabrous, the valves sometimes twisted at maturity, on an ascending or spreading pedicel 4–20 mm. long. Seeds pale brown, 1–2 mm. long. Gametic chromosome numbers, $n=7$, 14. Autogamous.

DISTRIBUTION: Sandy or clayey slopes and flats, from southeastern Oregon, southwestern and central Idaho, and western and central Wyoming, western Colorado, northeastern Arizona, and adjacent New Mexico, throughout Utah, and in northeastern Nevada. From 2,500–6,000 ft. alt.

13a. Camissonia scapoidea subsp. **scapoidea**

Oenothera scapoidea Torr. & Gray, Fl. N. Amer. 1: 506. 1840.

Chylisma scapoidea (Torr. & Gray) Small, Bull. Torrey Cl. 23: 193. 1896.

Oenothera brevipes var. *scapoidea* (Torr. & Gray) H. Lév., Monogr. Onoth. 146. 1905.

Chylismia scapoidea var. *seorsa* A. Nels., Bot. Gaz. 54: 140. 1912. Lectotype: Evanston, Uinta Co., Wyoming, 27 July 1897, *A. Nelson* 4125 (RM 10458).

Oenothera scapoidea var. *typica* Munz, Amer. Journ. Bot. 15: 233. 1928.

Oenothera scapoidea var. *seorsa* (A. Nels.) Munz, Amer. Journ. Bot. 15: 233. 1928.

Oenothera scapoidea subsp. *scapoidea* Raven, Univ. Calif. Publ. Bot. 34: 94. 1962.

Leaves usually simple, more rarely with a few reduced lateral leaflets, the blades narrowly ovate to ovate, often cordate at the base, to 5.5 cm. long and 3 cm. wide, subglabrous, very rarely villous on both surfaces, the oil cells below pale yellowish brown, rarely darker. Petals acute, 1.7–5 mm. long, 1.5–3.5 mm. wide, often red-dotted near the base. Filaments of the episepalous stamens 1–4 mm. long, those of the epipetalous ones 0.5–2.5 mm. long; anthers 0.5–1.9 mm. long, glabrous or ciliate. Style 2.5–9 mm. long. Capsule (1–)1.5–3 cm. long; pedicel 5–18 mm. long. Gametic chromosome numbers $n=7$, 14. Autogamous.

TYPE: Clay hills, probably near the rendezvous of 1834, on Ham's Fork of the Green River, Sweetwater County, Wyoming, 22 June to 2 July 1834, *T. Nuttall* (NY; isotypes BM, GH). See Raven, Univ. Calif. Publ. Bot. 34: 93. 1962.

DISTRIBUTION: Sandy or clay flats, throughout western Wyoming, west to Lake County, Oregon, and Elko and White Pine Counties,

Nevada, south to Beaver County, Utah, northern Coconino, Navajo, and Apache Counties, Arizona, San Juan County, New Mexico, and western Colorado; also on the headwaters of the Arkansas River in eastern Colorado. The only member of sect. *Chylismia* that occurs east of the Continental Divide. From 4,000–8,000 ft. alt.

Camissonia scapoidea subsp. *scapoidea* grows sympatrically with *C. eastwoodiae* and in the same vicinity as the ecologically distinct *C. walkeri* subsp. *walkeri*. It is highly variable, as would be expected in such widely ranging, principally autogamous entity. Both diploid and tetraploid populations occur in this taxon. The first series of tetraploids I studied (Univ. Calif. Publ. Bot. 34: 38–39. 1962), from Emery County, Utah, was growing with *C. eastwoodiae* and diploid plants of *C. scapoidea* subsp. *scapoidea*. At the time, it seemed possible that these tetraploids might have had an allopolyploid origin between the two diploids. It seemed even more likely, however, that they were autotetraploids derived from diploid *C. scapoidea* subsp. *scapoidea*, from which they were morphologically almost indistinguishable. This possibility is now considerably strengthened by the discovery of a tetraploid individual in Sweetwater County, Wyoming, along Interstate Hwy. 80, 4.8 miles southwest of junction with U.S. Hwy. 30N, R19544. This locality is some 150 miles north of the nearest station for *Camissonia eastwoodiae*. The plant examined formed 14 pairs of chromosomes, like the individuals from Utah studied earlier. A diploid individual was likewise found in southwestern Wyoming, 1.7 miles west of Fort Bridger, Uinta County, *Mosquin & Mulligan* 5128. These two chromosome counts constitute the first from the northern portion of the range of the subspecies and suggest the necessity for further chromosome counts of this taxon before its cytological pattern of variation can properly be assessed.

13b. Camissonia scapoidea subsp. **macrocarpa** (Raven) Raven, Brittonia 16: 282. 1964.

Oenothera scapoidea subsp. *macrocarpa* Raven, Univ. Calif. Publ. Bot. 34: 95. 1962.

Basal rosette compact, the leaves simple, rarely with reduced lateral leaflets. Leaf blades ovate, often cordate at the base, to 3.5 cm. long and 1.5 cm. wide, nearly glabrous, the oil cells below pale yellowish brown. Petals 1.5–2 mm. long, ca. 1.5 mm. wide. Filaments of the episepalous stamens ca. 2 mm. long, those of the epipetalous ones ca. 1 mm. long; anthers ca. 1 mm. long, ciliate. Style ca. 3 mm. long. Capsule 2.5–4 cm. long, stout, very large for size of plant, ascending; pedicel 4–6 mm. long. Autogamous.

TYPE: 9 miles northeast of Black Point, 5,700 ft., Apache County, Arizona, 11 June 1937, *R. H. Peebles & E. G. Smith* 13529 (US 1739264; isotypes, ARIZ, US).

DISTRIBUTION: On detrital clay knobs and gravelly flats, northern Apache and Navajo Counties and northeastern Coconino County, Arizona. From 5,000–6,500 ft. alt.

13c. Camissonia scapoidea subsp. **brachycarpa** (Raven) Raven, Brittonia 16: 282. 1964.

Oenothera scapoidea subsp. *brachycarpa* Raven, Univ. Calif. Publ. Bot. 34: 95. 1962.

Slender, the leaves simple or often pinnate with well-developed lateral leaflets. Terminal leaflets narrowly ovate, often cordate at the base, to 10 cm. long and 5 cm. wide, glabrous or weakly pubescent, the oil cells below dark brown, prominent. Petals 1.8–4 mm. long, acute, 1–4 mm. wide, often red-dotted near the base. Filaments of the episepalous stamens 1.2–3.2 mm. long, those of the epipetalous ones 0.5–1.5 mm. long; anthers 0.9–1.8 mm. long, ciliate. Style 4–7.5 mm. long. Capsule 0.8–2 (–2.8) cm. long; pedicel 10–16 mm. long. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Loose dry open slopes with sagebrush and shrubs, 7 miles north of Brogan, T. 14 S., R. 42 E., sec. 27, 3,000 ft., Malheur County, Oregon, 10 June 1955, *A. Cronquist* 7808 (NY; isotypes, DS, GH, ID, MO, RM, RSA, UC, US, UTC, WS, WTU).

DISTRIBUTION: Sandy slopes and flats, with *Grayia*, *Artemisia*, or *Juniperus*, southeastern Oregon, southwestern Idaho, northwestern Utah, and northeastern Nevada. From 2,500–6,000 ft. alt.

Camissonia scapoidea subsp. *brachycarpa* grows sympatrically with *C. claviformis* subsp. *cruciformis* and subsp. *integrior*, and overlaps morphologically with *C. scapoidea* subsp. *scapoidea*, from which it is separated geographically. The possible derivation of this species from populations similar to *C. claviformis* subsp. *cruciformis* and *C. eastwoodiae* has been discussed earlier (Raven, Univ. Calif. Publ. Bot. 34: 71. 1962).

13d. C. scapoidea subsp. **utahensis** (Raven) Raven, Brittonia 16: 282. 1964.

Oenothera scapoidea subsp. *utahensis* Raven, Univ. Calif. Publ. Bot. 34: 96. 1962.

Leaves pinnate, sparsely pubescent, the lateral leaflets well developed, up to 1 cm. long; terminal segment ovate, cordate at the base, up to 4.5 cm. long and 3 cm. wide, the oil cells below dark brown. Petals 4–5.5 (–8) mm. long, 3–4 mm. wide, blunt, often red-dotted near the base. Filaments of the episepalous stamens 5–6 mm. long, those of the epipetalous ones 3.5–4 mm. long; anthers 2–2.5 mm. long, ciliate. Style 8–11 mm. long. Capsule 1.6–3.8 cm. long; pedicel 8–20 mm. long. Autogamous.

TYPE: Black Rock, 4,300 ft., Salt Lake County, Utah, June 1869, *S. Watson* (US 70527; isotype, GH).

DISTRIBUTION: On dry rocky slopes and flats, with *Atriplex* and *Chrysothamnus*, western Utah and extreme northeastern Nevada (Elko County). From 4,100–5,500 ft. alt.

No new information is available about this enigmatic subspecies, which stands in an intermediate position, both morphologically and geographically, between *C. scapoidea* and *C. walkeri* subsp. *tortilis*.

14. Camissonia parryi (S. Wats.) Raven, Brittonia 16: 282. 1964.
Oenothera parryi S. Wats., Amer. Nat. 9: 270. 1875.
Oenothera scapoidea var. *parryi* (S. Wats.) M. E. Jones, Proc. Calif. Acad. II. 5: 682. 1895.
Oenothera tenuissima M. E. Jones, Proc. Calif. Acad. II. 5: 683. 1895. Type: In clay washes, Rockville, 4,000 ft., Washington Co., Utah, 26 September 1894, *M. E. Jones* 6083 (POM 38644; isotypes, MO, NY, UC, US).
Chylisma parryi (S. Wats.) Small, Bull. Torrey Cl. 23: 193. 1896.
Oenothera brevipes race *parryi* (S. Wats.) H. Lév., Monogr. Onoth. 146. 1905.
Chylismia tenuissima (M. E. Jones) Rydb., Bull. Torrey Cl. 40: 66. 1913.
Oenothera parryi f. *tenuissima* (M. E. Jones) Raven, Univ. Calif. Publ. Bot. 34: 111. 1962.

Erect and often intricately branched annual herb 5–80 cm. tall, with poorly defined basal rosette, densely covered below with white trichomes ca. 2 mm. long, forming a villous pubescence on the stems and leaves. Leaves simple or very rarely with a few small lateral leaflets, ovate, often cordate at the base, sparsely dentate, reduced upward, the veins below lined with pale or dark brown oil cells. Inflorescences nodding, mostly glabrous, with intricate, filiform branches, corymbiform. Hypanthium 0.5–2 mm. long, 0.3–0.5 mm. across at the summit, glabrous or villous without and within. Sepals 1.5–4 mm. long, 0.5–1.3 mm. wide, villous to glabrous, with clusters of light-brown oil cells at tip, the caudate appendages absent. Petals 2–7 mm. long, 2–6 mm. wide, bright yellow, of same color as stamens, style, and inside of hypanthium, often red-dotted near the base, sometimes fading rose. Filaments of the episepalous stamens 1.7–3.5 mm. long, those of the epipetalous ones 1.2–2.5 mm. long; anthers 0.9–1.2 mm. long, glabrous. Style 4–9 mm. long, glabrous; stigma 0.3–0.6 mm. thick, held well above the anthers at anthesis. Capsule 0.4–1 cm. long, 1.2–1.5 mm. thick, glabrous or glandular-pubescent, on a filiform pedicel 4–20 mm. long, the pedicel widely spreading or reflexed but the capsule erect. Seeds light brown, finely pitted, lenticular, with narrow cellular rim, few and crowded in 4-septate capsule so as to appear 1-rowed, 0.7–1.2 mm. long, 0.5–0.6 mm. thick. Gametic chromosome number, $n=7$. Outcrossing.

Type: Abundant on bare gypseous clay hills near St. George, Washington County, Utah, 1874, *C. C. Parry* 72 (GH; isotypes, DS, F, GH, MO, ND, NY).

Distribution: Red clay and sand slopes weathered from red (fresh-water-deposited) sandstone cliffs, with *Larrea* or *Juniperus*, southwestern Utah and northwestern Arizona. From 2,700–4,000 ft. alt.

FIGURE 6.—*Camissonia arenaria*, × ⅜ (*Raven* 11743, DS).

Camissonia parryi is highly restricted geographically and edaphically and distinctive morphologically. It no longer appears desirable to accord formal taxonomic recognition to the late season plants Jones described as *Oenthera tenuissima*. *Camissonia parryi* is very likely self-incompatible. It grows sympatrically with *C. multijuga*, but the

latter is confined to firm rock walls, whereas *C. parryi* grows on red-clay flats, which it often carpets.

15. Camissonia exilis (Raven) Raven, Brittonia 16: 383. 1964. FIGURE 7
Oenothera exilis Raven, Univ. Calif. Publ. Bot. 34: 114. 1962.

Slender and copiously branched, with purplish-brown stems, covered with glandular puberulence, and with occasional scattered white-villous pubescence. Leaves to 3.5 cm. long, reduced upward, with narrowly ovate blades to 2 cm. long and 0.7 cm. wide, the margins feebly denticulate, the veins below lined with brownish oil cells. Inflorescence erect, sparse, elongating in fruit, each flower subtended by a bract to 3.5 mm. long, with a petiole to 1 mm. long. Hypanthium 0.4–0.5 mm. long, 0.4 mm. across at the summit, glabrous within. Sepals 1–1.2 mm. long, ca. 0.5 mm. wide, with small clusters of oil cells at apices. Petals 1–1.5 mm. long, ca. 1 mm. wide, yellow fading purplish, the same color as stamens, style, and inside of hypanthium. Stamens 4, episepalous; filaments ca. 0.5 mm. long; anthers ca. 0.5 mm. long, glabrous. Style ca. 1.5 mm. long, glabrous; stigma ca. 0.2 mm. thick, surrounded by the anthers at anthesis. Capsule 0.45–0.7 cm. long, ca. 1.5 mm. thick, clavate; pedicel 4–9 mm. long; pedicels spreading, the capsules spreading or ascending. Seeds light brown, ca. 0.8 mm. long, ca. 0.5 mm. wide. Gametic chromosome number, $n=7$. Autogamous.

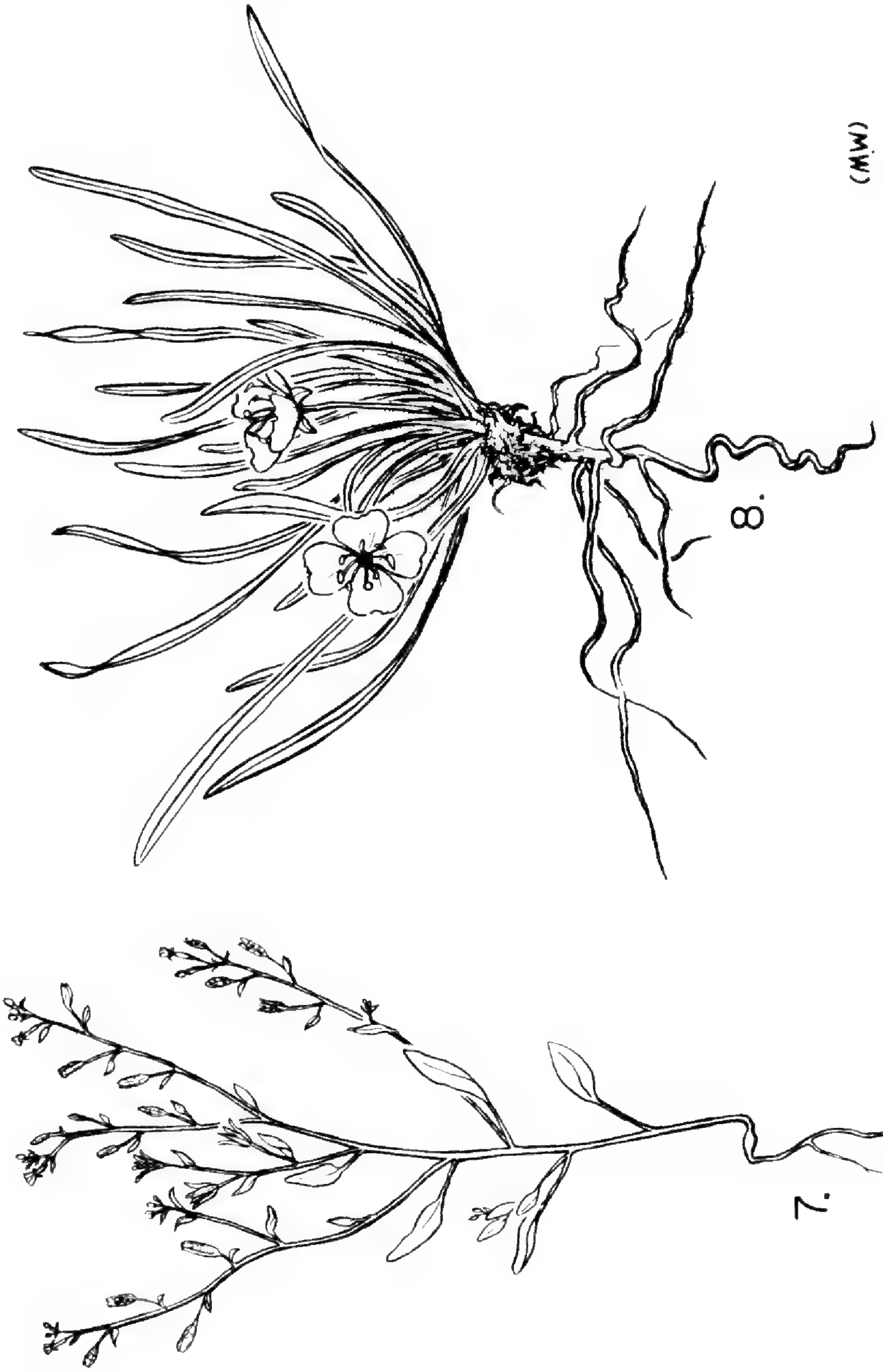
TYPE: "Gypsum-covered flat," near Cottonwood Spring, east base of Virgin Mountains, 3,500 ft., Mohave County, Arizona, 6 June 1941, *P. A. Munz* 16779 (POM 264197; isotype, DS).

DISTRIBUTION: Travertine-covered flats, east base of Virgin Mountains, ca. 3,500 ft., Mohave County, Arizona; Buckskin Mountains, between Willow Springs and Lees Ferry, ca. 5,000 ft., Coconino County, Arizona.

This exceedingly rare and local species is the only member of the genus characterized by the absence of the epipetalous stamens. On the other hand, certain plants of *C. andina* have also lost this whorl of stamens, and the epipetalous stamens are sometimes greatly reduced in *C. minor*. In all other respects, *C. exilis* is closely similar to *C. parryi* and to other species of sect. *Chylismia*, and I no longer recognize it as constituting a distinct, monotypic section, which procedure would confer undue emphasis to a single distinctive characteristic.

16. Camissonia megalantha (Munz) Raven, Brittonia 16: 282. 1964.
Oenothera heterochroma var. *megalantha* Munz, Leafl. West. Bot. 3: 52. 1941.
Oenothera megalantha (Munz) Raven, Univ. Calif. Publ. Bot. 34: 111. 1962.

Robust annual with glandular pubescence, 0.1–2 m. tall, with an ill-defined basal rosette, the cauline leaves larger below; secondary branches numerous. Leaves simple, broadly ovate, cordate at the



FIGURES 7–8.—Species of *Camissonia*, × ¾: 7, *C. exilis* (*Munz* 16779, isotype, DS); 8, *C. graciliflora* (*Bacigalupi* 1096, DS).

base, sinuate-dentate, the veins below prominently lined with yellowish oil cells, the blades up to 8 cm. long and 7 cm. wide, the petioles to 5.5 cm. long. Hypanthium 4.5–8.5 mm. long, 1.5–3 mm. across at the summit, glandular-pubescent without, cream (greenish yellow near summit) with matted villous pubescence within, except for the glabrous lower 2 mm. Sepals 4.5–9 mm. long, 1.5–2.4 mm. wide, with clusters of oil cells at the apices, often reflexed in pairs; caudate appendages absent. Petals 9–13.8 mm. long, 6–15.5 mm. wide, pale to dark lavender, diffusely flecked with purplish near the base, and white at the very base. Filaments pale greenish yellow, those of the episepalous stamens 6–12 mm. long, those of the epipetalous ones 3.5–8 mm. long; anthers ca. 2 mm. long, glabrous. Style 14–22.5 mm. long, white, densely villous above the lowest 3–4 mm., up to a point above the summit of the hypanthium (ca. 5–5.5 mm. below the stigma); stigma depressed-globose, ca. 1 mm. across, ca. 0.5 mm. high, held well above the anthers at anthesis. Capsule 0.8–1.4 cm. long, 1.3–2 mm. thick, clavate; pedicel 2–3.5 mm. long. Seeds brown, 1–1.3 mm. long. Gametic chromosome number, $n=7$. Outcrossing but self-compatible.

TYPE: Volcanic alkali soil, Cane Springs, Skull Mountains, Nye County, Nevada, 24 August 1938, *P. Train* 2358 (POM 253923; isotypes, ARIZ, CAS, DS).

DISTRIBUTION: Known only from rubble derived from volcanic tuff, partly on moist soil about springs, at the type locality, at ca. 4,100 ft. alt., in southern Nye County, Nevada. Flowering mostly from June to October; germinating in the late spring.

Camissonia megalantha is outcrossed and visited by such large, polylectic bees as *Anthophora urbana* Cress. and *Centris rhodopus* Ckll. soon after its flowers open near sunrise (Raven, MS.). It is, however, self-compatible, as shown by comparative studies of pollen-tube growth in 46 selfed and outcrossed individuals from the type locality. This species and its obvious derivative, the autogamous *C. heterochroma*, are the only lavender-flowered species in the genus *Camissonia*, and two of the very few that regularly bloom in the autumn. They are highly specialized vegetatively within this group. In the tribe Onagreae, species with lavender or purplish petals are found in the following genera: *Gongylocarpus*, *Clarkia*, *Heterogaura*, and *Oenothera*. In species of most genera, however, the petals may fade purplish after fertilization, indicating that the capability of producing such pigments exists throughout the tribe. *Camissonia megalantha* occurs sympatrically with *C. claviformis* subsp. *claviformis*.

17. Camissonia heterochroma (S. Wats.) Raven, Brittonia 16: 282. 1964.
Oenothera heterochroma S. Wats., Proc. Am. Acad. 17: 373. 1882.
Chylisma heterochroma (S. Wats.) Small, Bull. Torrey Cl. 23: 193. 1896.
Oenothera heterochroma var. *typica* Munz, Aliso 2: 83. 1949.

Oenothera heterochroma var. *monoensis* Munz, Aliso 2: 84. 1949. Type: Sherwin Grade, 5,500 ft., Mono Co., California, 16 August 1947, *J. T. Howell* 24172 (CAS 342092; isotypes, DS, RSA).

Oenothera heterochroma subsp. *heterochroma* Raven, Univ. Calif. Publ. Bot. 34: 112. 1962.

Oenothera heterochroma subsp. *monoensis* (Munz) Raven, Univ. Calif. Publ. Bot. 34: 113. 1962.

Annual herb 0.1–1 m. tall, with an ill-defined basal rosette; secondary branches numerous; entire plant covered with glandular pubescence, or nearly glabrous and glaucous above. Leaves simple, ovate, often cordate at the base, sinuate-dentate, glandular-pubescent, to 7 cm. long and 5 cm. wide, the veins below prominently lined with brown oil cells, the petioles to 6 cm. long. Inflorescences erect, elongating in flower, mostly axillary. Hypanthium 2–5 mm. long, 0.5–1.7 mm. wide at the summit, glandular-pubescent without, villous within. Sepals 1.5–3.5 mm. long, 0.6–1.5 mm. wide, with clusters of oil cells at tips; caudate appendages absent. Petals 2–6 mm. long, 1–4 mm. wide, lavender, paler below, often yellow at very base and often with lavender flecks below. Filaments creamy, those of the episepalous ones 1.8–3 mm. long, those of the epipetalous ones 1–2.5 mm. long; anthers 0.6–1 mm. long, glabrous or sparsely ciliate. Style creamy, villous near the base, 4–7 mm. long, stigma ca. 0.8–1 mm. thick, surrounded by the anthers at anthesis. Capsule 0.7–1.3 cm. long, 1.3–2 mm. thick, erect, clavate, straight, glandular-pubescent; pedicel 2–5 mm. long. Seeds brown, 1–1.2 mm. long. Gametic chromosome number, $n=7$. Autogamous.

Type: Candelaria, Mineral County, Nevada, 1881, *W. H. Shockley* 19 (GH).

Distribution: Alluvial slopes and rocky slides, often on rocky soil, Churchill and Lander Counties, Nevada, south to Lincoln and southern Nye Counties, Nevada, Mono Lake, Mono County, and central Inyo County, California. From 2,200–7,000 ft. alt.

Camissonia heterochroma is highly colonial, rare, and autogamous. Although it grows adjacent to *C. brevipes* subsp. *brevipes*, *C. claviformis* subsp. *funerea*, *C. claviformis* subsp. *integrior*, *C. claviformis* subsp. *lancifolia*, and *C. munzii*, its time of flowering only rarely coincides with that of any of these entities. I can no longer see any justification for separating the relatively glabrous and glaucous populations within this species (=subsp. *monoensis*) as a separate entity, particularly in view of their poorly separated geographical ranges; plants from Lincoln County, Nevada, are more or less intermediate in pubescence characters.

The following two collections, seen since I completed my revision of the group in 1962, extend the then known range: Cerro Gordo, 3.8 miles east of Keeler, Inyo Mountains, Inyo County, ca. 5,300 ft.,

California, *Thompson* 3383 (DS); east side road south of Rainier Mesa, 5.4 miles north of junction of Tippipah Road, East Forty-Mile Drainage, 5,000 ft., Nye County, Nevada, *Beatley* 391 (DS).

Section III. *Lignothera*

Oenothera subg. *Chylismia* sensu Munz, Amer. Journ. Bot. 16: 224. 1929; N. Amer. Fl. II. 5: 163. 1965; pro parte.
Oenothera sect. *Euchylismia* sensu Munz, Amer. Journ. Bot. 16: 224. 1929; pro parte.
Oenothera sect. *Lignothera* Raven, Univ. Calif. Publ. Bot. 34: 76. 1962.
Camissonia sect. *Lignothera* (Raven) Raven, Brittonia 16: 281. 1964.

Suffrutescent perennials, flowering the first year, the plants caulescent, not flowering at the basal nodes. Inflorescence nodding. Flowers opening in the late afternoon. Ovary lacking a sterile projection. Hypanthium lacking a fleshy disc within. Sepals reflexed separately. Petals dull yellow or rarely cream, unmarked, fading brick red or yellowish, with no contrasting ultraviolet-reflective pattern. Stamens and style yellow, the stigma depressed globose, greenish yellow. Stamens 8, subequal; anthers versatile, ciliate. Pollen shed in tetrads. Capsule subsessile or with a prominent, stout pedicel, straight or slightly curved, subterete, the seeds in 2 rows in each locule. Seeds monomorphic, narrowly obovoid, finely lacunose.

Type species: *Camissonia cardiophylla* (Torr.) Raven.

Distribution: Alluvial slopes and washes from Inyo County, California, south through San Diego County, California, and Pinal County, Arizona, to northwestern Sonora and about 27°50′ N. lat. in Baja California; Isla de Cedros and islands in the Golfo de California.

In 1962, I regarded this group as an early evolutionary offshoot within *Camissonia* (Univ. Calif. Publ. Bot. 34: 67). In my present view, however, it is more logical to regard the late afternoon opening of the flowers, pollen shed in tetrads, and perhaps woody habit as specializations within the tribe Onagreae, and consequently to regard sect. *Lignothera* as a specialized offshoot of some species similar to the relatively generalized ones in sect. *Chylismia*. The hypanthium in plants of sect. *Lignothera* is not approached in length by any other species of *Camissonia*, and it now appears likely that the two closely related species comprising this group are best regarded as primarily moth-pollinated derivatives in a mainly bee-pollinated (and morning-opening) group. Hawk-moth pollination is probably important here, particularly with respect to *C. arenaria*, in which the hypanthium may be up to 4 cm. long. The relationship of sect. *Lignothera* to the remainder of *Camissonia* might therefore be analogous to the relationship between the hawk-moth-pollinated *Gaura mutabilis* Cav. and the rest of the genus *Gaura*. There seems to be no reason to regard the shedding of pollen in tetrads as primitive in the tribe Onagreae or in

the family, and relatively generalized species of sect. *Eulobus* and sect. *Chylismia* are somewhat woody.

Of the 36 plants of sect. *Lignothera* for which chromosome number determinations have been made, pairing has been observed in 30. Two of these had a ring of 4, and one had 2 rings of 4. Thus 10 percent of the plants examined were chromosomally heterozygous, which is a relatively high proportion but much lower than that found in sect. *Chylismia*.

18. Camissonia cardiophylla (Torr.) Raven, Brittonia 16: 281. 1964.

Plants to 1 m. tall, covered with villous or glandular pubescence. Leaves reduced upward, ovate to cordate-orbicular, blades to 5.5 cm. long and 5.5 cm. wide, pubescent, erose-dentate, the teeth tipped with clusters of brown oil cells, the petioles to 7.5 cm. long. Hypanthium 4.5–14 mm. long, 3–7 mm. across at the summit, villous within, pubescent without; sepals 3–9 mm. long, 2–3.5 mm. wide. Petals 3–12 mm. long, 2–13 mm. wide, yellow or cream. Filaments 1–3 mm. long; anthers 2–4 mm. long. Style 8–23 mm. long, stigma 2–3.5 mm. thick surrounded by or held just above the anthers at anthesis. Capsule 2–5.5 cm. long, 2.5–3.5 mm. thick, straight or slightly curved, ascending; pedicel 1–18 mm. long. Seeds 0.5–0.7 mm. long. Gametic chromosome number, $n=7$. Self-compatible but often outcrossing.

DISTRIBUTION: Alluvial slopes and washes from Inyo County, California, south through San Diego County, California, and Pinal County, Arizona, to 27°50′ N. lat. in Baja California. Also on Isla de Cedros and on several islands in the Golfo de California, both in Baja California and in Sonora. From sea level to 4,500 ft. alt. See Univ. Calif. Publ. Bot. 34: *fig. 1*. 1962.

18a. Camissonia cardiophylla subsp. **cardiophylla**

Oenothera cardiophylla Torr., Pac. R. R. Rep. 5: 360. 1858.

Oenothera cardiophylla var. *petiolaris* M. E. Jones, Proc. Calif. Acad. II, 5: 682. 1895. Lectotype: Rosario Mission, Baja California, 30 April 1886, *C. R. Orcutt* 1333 (US 47096; isotypes, F, GH, MO, NY, PH).

Chylismia cardiophylla (Torr.) Small, Bull. Torrey Cl. 23: 193. 1896.

Oenothera cardiophylla var. *typica* Munz, Amer. Journ. Bot. 15: 226. 1928.

Oenothera cardiophylla subsp. *cardiophylla*; Raven, Univ. Calif. Publ. Bot. 34: 78. 1962.

Pubescence villous, sometimes glandular, often mixed. Leaves cordate. Hypanthium 4.5–12 mm. long, villous or more rarely glandular-pubescent without. Petals 3–12 mm. long, 2–12 mm. wide. Style 8–23 mm. long, often held above the anthers at anthesis. Gametic chromosome number, $n=7$. Self-compatible but often outcrossing.

TYPE: Fort Yuma, Yuma County, Arizona, *Major G. H. Thomas* (NY).

DISTRIBUTION: Rocky walls and sandy alluvial flats with *Hyptis emoryi*, *Larrea* and *Ambrosia dumosa*, southern San Bernardino County, California, south to eastern San Diego County, California, and Yuma County (and possibly western Pinal County), Arizona, and south in northeastern and central Baja California, Mexico, to approximately 27°50′ N. lat.; also on Isla Angel de la Guarda, Isla San Marcos, Isla San Luis, Isla San Pedro Mártir, and Isla San Esteban in the Golfo de California. Isla San Esteban is the only locality for this subspecies in Sonora. From sea level to 2,000 ft. alt. See Univ. Calif. Publ. Bot. 34: *fig. 1*. 1962.

Progeny of *Balls & Everett* 22918, grown at Claremont, California, were self-compatible, as were two individuals from Yaqui Pass, San Diego County, California, *Kyhos* 64–6, judging by pollen-tube growth in selfed individuals, and two from Box Canyon, Riverside County, California, *Kyhos* 65–109 (DS). Gametic chromosome counts of $n=7$ have recently been made in two collections from Mexico: Isla San Esteban, Golfo de California, Sonora, *Moran* 13047; Las Trincheras, 28°29′ N. lat., 113°07′ W. long., ca. 430 m., Baja California, *Moran* 12600. *Wiggins* 18159 (DS), from 41 miles south of San Felipe, Baja California, represents a previously unreported station for this taxon. *Camissonia cardiophylla* subsp. *cardiophylla* has been found growing sympatrically with *C. arenaria*, with no evidence of hybridization.

18b. Camissonia cardiophylla subsp. **robusta** (Raven) Raven, Brittonia 16: 281. 1964.

Oenothera cardiophylla subsp. *robusta* Raven, Univ. Calif. Publ. Bot. 34: 79. 1962.

Entire plant glandular-pubescent and with scattered long, white, eglandular trichomes. Leaves broadly ovate, often cordate at the base, the petioles stout. Hypanthium 9–14 mm. long, glandular-pubescent without. Petals 7–11 mm. long, 9–13 mm. wide. Style 14–20 mm. long, the stigma usually held above the anthers at anthesis. Gametic chromosome number, $n=7$. Self-compatible but often outcrossed.

TYPE: Rocky canyon slopes, Jail Canyon, west slope of Panamint Range, 2,500 ft., Inyo County, California, 14 April 1937, *P. Train* (US 1737210; isotypes, ARIZ, COLO, DS, NA, OSC, UC).

DISTRIBUTION: Rocky borders of washes and hillsides, with *Larrea* and *Ambrosia dumosa*, western and southern margins of Death Valley, Inyo County, California. From 2,000–4,500 ft. alt. See Univ. Calif. Publ. Bot. 34: *fig. 1*. 1962.

Camissonia cardiophylla subsp. *robusta* is presumably self-compatible, as isolated individuals have on two occasions been observed setting fruit.

18c. Camissonia cardiophylla subsp. **cedrosensis** (Greene) Raven, Brittonia 16: 281. 1964.

Oenothera cedrosensis Greene, Bull. Calif. Acad. 1: 187. 1885.

Oenothera cardiophylla subsp. *cedrosensis* (Greene) Raven, Univ. Calif. Publ. Bot. 34: 79. 1962.

Mostly annual, the plants entirely glandular-pubescent, with scattered long, eglandular trichomes. Leaves ovate, acuminate at the apex, much longer than broad, broadly cuneate or very rarely slightly cordate at the base. Hypanthium 8–12 mm. long, glandular-pubescent without. Petals cream or even (?) white, 3–4.5 mm. long, 3–4 mm. wide. Style 10–15 mm. long; stigma surrounded by the anthers at anthesis. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Isla de Cedros, Baja California, 1859, *J. A. Veatch* (CAS 862).

DISTRIBUTION: Arroyos and borders of washes, with *Pachycormus*, *Larrea*, *Pachycereus*, and *Bursera*, Isla de Cedros west to Bahía de los Angeles and El Desierto Vizcaíño, Baja California; Isla Tiburón, Sonora. From near sea level to perhaps 1,000 ft. alt. See Univ. Calif. Publ. Bot. 34: *fig. 1*. 1962.

Camissonia cardiophylla subsp. *cedrosensis* is local and apparently not common. This entity is undoubtedly more highly self-pollinating than the other races of this self-compatible species, judging from its smaller flowers. A plant from Bahía de los Angeles, Baja California, *Moran* 12419, had 7 pairs of chromosomes at meiotic metaphase I.

19. Camissonia arenaria (A. Nels.) Raven, Brittonia 16: 281. 1964. FIGURE 6

Chylisma arenaria A. Nels., Amer. Journ. Bot. 21: 575. 1934.

Oenothera cardiophylla var. *splendens* Munz & Johnst., Bull. Torrey Cl. 49: 354. 1923. Type: UC 196590, with same data as type of *Oenothera cardiophylla* var. *longituba* Jeps.; not located.

Oenothera cardiophylla var. *longituba* Jeps., Man. Fl. Pl. Calif. 686. 1925. Type: High among rocks at the foot of the Needles, Colorado R., Mohave Co., Arizona, 7 March 1910, *J. Grinnell* (JEPS 2668); see above.

Oenothera arenaria (A. Nels.) Raven, Univ. Calif. Publ. Bot. 34: 76. 1962.

Plants to 1.8 m. tall, villous, occasionally with scattered glandular trichomes in the inflorescence. Leaves reduced upward, the petioles to 6 cm. long, the blades to 6 cm. long and 6 cm. wide, villous above and densely so below, ovate, cordate at the base, the apex sometimes acuminate, coarsely dentate or doubly dentate. Inflorescence less compact than that of *C. cardiophylla*. Hypanthium 18–40 mm. long, 5–8 mm. across at the summit, villous without, finely pubescent within. Sepals 8–15 mm. long, 3–5.5 mm. wide. Petals 8–20 mm. long, 7–28 mm. wide. Filaments 5–9 mm. long; anthers 5–8 mm. long. Style 30–58 mm. long; stigma 2.5–3 mm. thick, held above the anthers at anthesis. Capsule 3–4.4 cm. long, 2.5–3.5 mm. thick; pedicel 2–5 mm. long. Seeds 0.5–0.7 mm. long. Gametic chromosome number, $n=7$. Outcrossed.

TYPE: Sandy washes in the Fortuna Range (western Gila Mountains), ca. 20 miles east of Yuma, Yuma County, Arizona, 26 February 1930, *A. Nelson* 10140 (RM 138602).

DISTRIBUTION: Sandy washes, rocky conglomerate cuts, and granitic slopes and draws, with *Larrea*, *Prosopis*, *Carnegiea*, and *Ambrosia dumosa*, foot of the Needles, Mohave County, Arizona; from the north end of the Salton Sea, Riverside County, California, southeastward to the Tinajas Atlas Range, Arizona and Sonora. From below sea level to 1,400 ft. alt. See Univ. Calif. Publ. Bot. 34: *fig. 1*. 1962.

This species has twice been found growing sympatrically with *C. cardiophylla* subsp. *cardiophylla*, but no intermediates have been observed.

Section IV. *Tetrapteron*

Oenothera subg. *Heterostemon* Nutt., Journ. Acad. Sci. Philad. 7: 22. 1834. Type: *Oenothera heterantha* Nutt. = *Camissonia subacaulis* (Pursh) Raven.

Oenothera subg. *Primulopsis* Torr. & Gray, Fl. N. Amer. 1: 507. 1840; nom. subs.

Oenothera subg. *Taraxia* Nutt. ex. Torr. & Gray, Fl. N. Amer. 1: 506. 1840. Lectotype: *Oenothera breviflora* Torr. & Grya = *Camissonia breviflora* (Torr. & Gray) Raven.

Taraxia (Nutt. ex. Torr. & Gray) Raimann, *in* Engl. & Prantl, Natürl. Pflanzenfam. III. 7: 216. 1893.

Oenothera sect. *Tetrapteron* Munz, Amer. Journ. Bot. 16: 247. 1929.

Oenothera sect. *Eutaraxia* Munz, Amer. Journ. Bot. 16: 247. 1929.

Oenothera sect. *Heterostemon* (Nutt.) Munz, N. Amer. Fl. II. 5: 143. 1965.

Ferennials or annuals, the plants acaulescent or subacaulescent with a crown of leaves and flowers at summit of the taproot. Flowers opening near sunrise. Ovary with a long, slender, sterile projection below the hypanthium on which the flower is placed. Hypanthium closed by an evident fleshy disc. Sepals reflexed separately or in pairs. Petals yellow, unspotted, strongly ultraviolet reflective, with a large non-reflective area near the base in *C. ovata*. Stamens, style, and inside of the hypanthium yellow, the stigma greenish yellow. Anthers attached near the base, erect in anthesis. Pollen shed singly. Capsule subsessile, irregularly loculicidal, the seeds in two rows in each locule, these rows often much crowded. Seeds monomorphic, with a linear raphe on one side, variable.

LECTOTYPE SPECIES: *Camissonia graciliflora* (Hook. & Arn.) Raven (cf Raven, Brittonia 16: 283. 1964).

DISTRIBUTION: South-central British Columbia and Alberta at about 51° N. lat. and southwestern Saskatchewan, and from the region of the Continental Divide westward south to southern Utah, central Nevada, and throughout California to northwestern Baja California.

This section of six species consists of four groups very distinct from one another: *C. ovata*, *C. subacaulis*, *C. tanacetifolia-C. breviflora*, and *C. graciliflora-C. palmeri*. The last two species are annual, the

others perennial. In view of their habit and clearly specialized capsules, it is believed that *C. graciliflora* and *C. palmeri* were derived from a perennial stock; but they are not especially similar to any of the extant perennials. *Camissonia ovata* and *C. tanacetifolia* consist largely or entirely of self-incompatible individuals, whereas *C. subacaulis* and *C. graciliflora* are facultatively outcrossed although self-compatible. *Camissonia breviflora* and *C. palmeri* are rather obviously specialized autogamous derivatives of species similar to *C. tanacetifolia* and *C. graciliflora*, respectively. Five of the six species in this section are diploid ($n=7$) but *C. tanacetifolia* is primarily tetraploid ($n=14$), with a local hexaploid ($n=21$) race and at least one diploid ($n=7$) population. A further discussion of chromosomal evolution in this species is included following its taxonomic description (p. 247).

Chromosomal heterozygosity is unknown in natural populations of this section, for which 173 diploid counts are available. Multivalent associations in the 25 tetraploid and 4 hexaploid plants of *C. tanacetifolia* examined clearly reflect autopolyploid pairing, not structural rearrangement.

20. Camissonia ovata (Nutt. ex Torr. & Gray) Raven, Brittonia 16: 283. 1964.

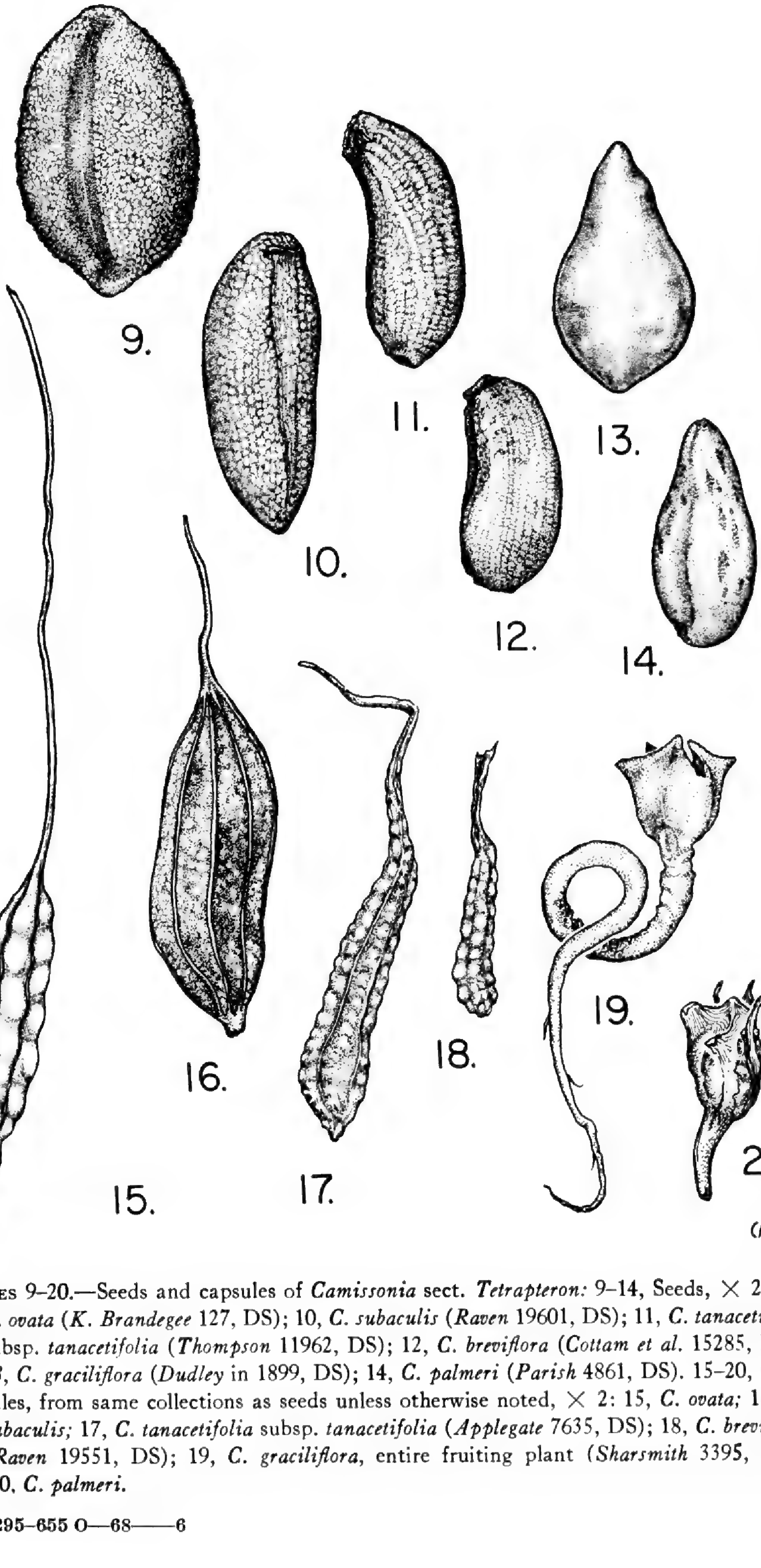
FIGURES 9, 15

Oenothera ovata Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 507. 1840. Munz, Amer. Journ. Bot. 16: 251. 1929; N. Amer. Fl. II. 5: 144. 1965.

Taraxia ovata (Nutt. ex Torr. & Gray) Small, Bull. Torrey Cl. 23: 185. 1896.

Oenothera primuloidea H. Lév., Monogr. Onoth. 65. 1902.

Subsucculent acaulescent perennial from a thick taproot which often branches at the crown in age. Leaves ovate to very narrowly elliptic, 3–15 cm. long, 1.6–5 cm. wide, more or less densely white-ciliate with erect trichomes ca. 0.5 mm. long, subentire to shallowly sinuate or crisped, rarely deeply sinuate, the apex acute to acuminate, the base attenuate to a narrowly winged petiole 8–150 mm. long, slightly dilated at the base. Buds erect just before anthesis. Sterile prolongation of ovary 2.5–18 cm. long. Hypanthium 2–3 mm. long, 3.5–5 mm. across at the summit, sparsely pubescent outside, with short matted trichomes inside near the base. Sepals 11–19 mm. long, 1.2–4 mm. wide, sparsely pubescent, reflexed separately. Petals often apiculate, 8–23 mm. long, 5–19 mm. wide. Filaments of the episepalous stamens 3.5–8 mm. long, those of the epipetalous ones 2–6 mm. long; anthers 3–4.8 mm. long. Style 4.5–11 mm. long, short-pubescent near the base; stigma 0.8–2 mm. in diameter, held slightly above the anthers at anthesis. Capsule 11–30 mm. long, 3–5 mm. thick, subterete, the walls thin, much distended by the seeds, rarely with a pedicel up to 0.4 mm. long. Seeds elongate-ovoid, uniform brown, densely and coarsely papillose, 1.8–2.2 mm. long, 1.2–1.4 mm. thick. Gametic chromosome number, $n=7$. Self-incompatible.



FIGURES 9–20.—Seeds and capsules of *Camissonia* sect. *Tetrapteron:* 9–14, Seeds, × 20: 9, *C. ovata* (*K. Brandegee* 127, DS); 10, *C. subaculis* (*Raven* 19601, DS); 11, *C. tanacetifolia* subsp. *tanacetifolia* (*Thompson* 11962, DS); 12, *C. breviflora* (*Cottam et al.* 15285, DS); *13, C. graciliflora* (*Dudley* in 1899, DS); 14, *C. palmeri* (*Parish* 4861, DS). 15–20, Capsules, from same collections as seeds unless otherwise noted, × 2: 15, *C. ovata;* 16, *C. subaculis;* 17, *C. tanacetifolia* subsp. *tanacetifolia* (*Applegate* 7635, DS); 18, *C. breviflora* (*Raven* 19551, DS); 19, *C. graciliflora,* entire fruiting plant (*Sharsmith* 3395, DS); 20, *C. palmeri.*

295–655 O—68——6

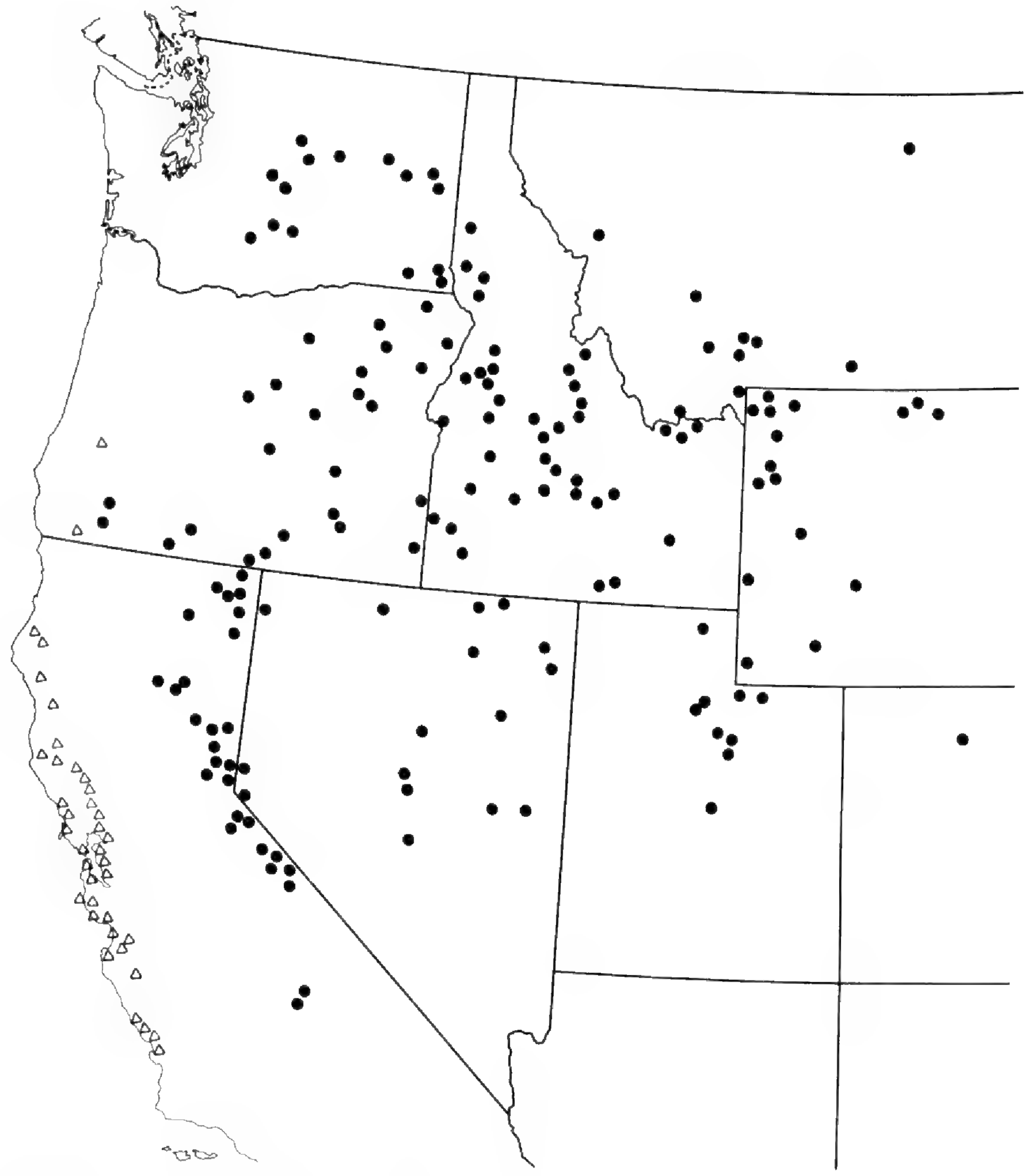
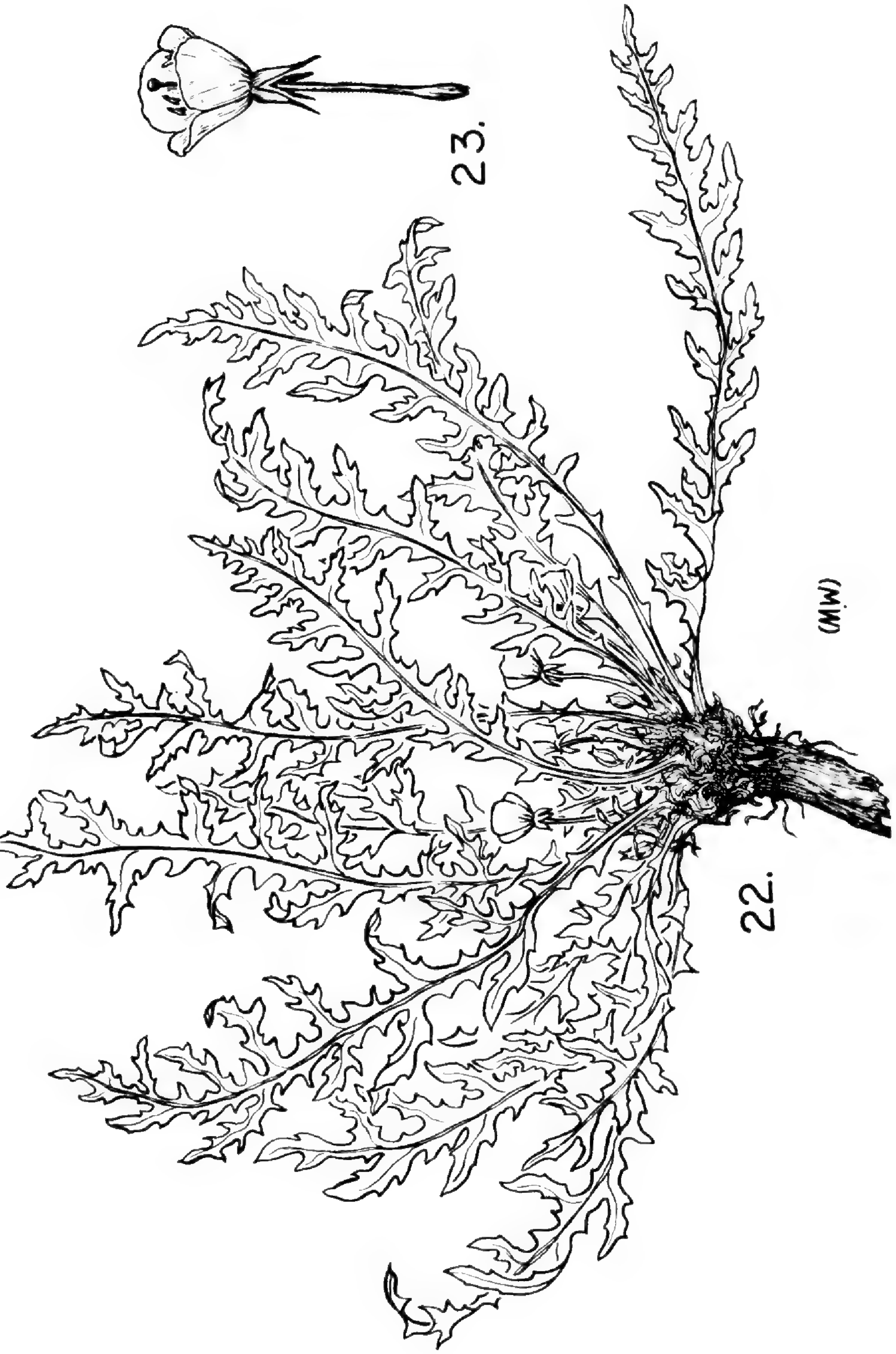


FIGURE 21.—Western United States, showing ranges of *Camissonia* sect. *Tetrapteron*: △=*C. ovata*; ●=*C. subacaulis*.

TYPE: Moist plains in the immediate vicinity of Monterey, Monterey County, Calif., March 1836, *T. Nuttall* (NY; isotypes, BM, GH).

DISTRIBUTION (Figure 21): Grassy fields, often in clay soil, not far from the coast; Umpqua Valley, Douglas County and Josephine County, Oregon; Humboldt, Mendocino, and Lake Counties south to the vicinity of Monterey Bay, Monterey County and again south of the Santa Lucia Mountains in northern San Luis Obispo County, from about 2 miles north of the mouth of Arroyo de la Cruz south to Los Osos Valley near Morro Bay, California. From sea level to about 1,500 ft. alt.



FIGURES 22–23.—Species of *Camissonia* sect. *Tetrapteron*, × ¾: 22, Plant of *C. breviflora* (Cottam *et al.* 15825, DS); 23, flower of *C. tanacetifolia* subsp. *tanacetifolia* (Thompson 11953, DS).

Vouchers for chromosome number, $n=7$ (no structural heterozygosity observed; 10 individuals, 7 populations):

U.S.: CALIFORNIA: LAKE CO.: 0.8 mi. W. of Lakeport, *Breedlove* 4567. MONTEREY CO.: Carmel Valley, R18148; 7 mi. SW. of San Juan Bautista on Old San Juan Grade, R18194. SAN BENITO CO.: 1 mi. W. of San Juan Bautista, R18193. SAN LUIS OBISPO CO.: 1 mi. N. of Cambria, R18140; 1 mi. S. of Cambria, R18747 (4 plants). SAN MATEO CO.: Pigeon Point, *Ornduff* 4746.

Individuals of *Camissonia ovata* are self-incompatible (contrary to the assertion of Katherine Brandegee, Univ. Calif. Publ. Bot. 6: 46. 1914), as judged by the lack of pollen-tube growth in 71 selfed individuals from a population near the intersection of Sand Hill Road and Whiskey Hill Road, near Woodside, San Mateo County, California; 7 individuals from the Lake County, California, population cited above, and 12 plants from the population from south of Cambria, San Luis Obispo County, California, cited above. I am grateful to Gretchen M. Mills for these observations on the San Mateo County population. *Camissonia ovata* has been found growing sympatrically with *C. graciliflora*. The oligolectic bee *Andrena* (*Diandrena*) *chalybea* (Cress.) is consistently associated with it throughout its range and usually effects pollination in the early morning (MacSwain, Raven & Thorp, MS.). Other species of bees gather pollen from *Camissonia ovata* and visit it locally, sometimes in competition with *Andrena chalybea*.

This species might possibly occur or have occurred in the Sierra Nevada foothills of central California, judging from a specimen labeled "Roseville, May 1884, M.K.C." (DS); it is uncertain whether the record refers to the community of this name in Sacramento County, California. At any rate, the occurrence of this species east of the Sacramento Valley has not been confirmed by modern collections.

The chromosome number of this species was earlier reported by Johansen (Amer. Journ. Bot. 16: 597. 1929; Ann. Bot. 45: 111–124, *pl. 6*. 1931), but without any definite indication of locality or voucher specimen.

Camissonia ovata is a distinctive species without any close relatives. It might be confused superficially with *C. subacaulis*, but the structure of the capsules and seeds in these two species is very different (figs. 9, 10, 15, 16), as is the marking of the petals when viewed in ultraviolet light. White-flowered plants are found in a very low frequency.

21. Camissonia subacaulis (Pursh) Raven, Brittonia 16: 283. 1964.

FIGURES 10, 16

Jussiaea subacaulis Pursh, Fl. Amer. Sept. 1: 304. 1814.

Oenothera heterantha Nutt., Journ. Acad. Philad. 7: 22. 1834. Type: Near Camas Creek, in or near Jefferson Co., Idaho, 23 June 1833, *N. J. Wyeth* (PH; isotypes, BM, NY).

Oenothera heterantha var. *taraxacifolia* S. Wats., Proc. Amer. Acad. 8: 589. 1873. Type: Near Austin, Lander Co., Nevada, July 1868, *S. Watson* (GH).
Taraxia heterantha (Nutt.) Small, Bull. Torrey Cl. 23: 186. 1896.
Taraxia heterantha var. *taraxacifolia* (S. Wats.) Small, Bull. Torrey Cl. 23: 186. 1896.
Taraxia taraxacifolia (S. Wats.) Heller, Muhlenbergia 1: 1. 1900.
Taraxia subacaulis (Pursh) Rydb., Mem. N.Y. Bot. Gard. 1: 281. 1900.
Oenothera primuloidea H. Lév., Monogr. Onoth. 65. 1902, pro parte; nom. subs.
Oenothera subacaulis (Pursh) Garrett, Spr. Fl. Wasatch 64. 1911.
Oenothera subacaulis var. *taraxacifolia* (S. Wats.) Jeps., Man. Fl. Pl. Calif. 683. 1925.

Subsucculent acaulescent perennial from a deep, thick taproot which may branch in age to produce more than a single rosette. Leaves lanceolate to narrowly elliptic, 2–22 cm. long, 0.7–4.2 cm. wide, rarely minutely and sparsely strigulose along veins and margins, subentire to sinuate or less commonly deeply and irregularly pinnatifid, the apex acuminate, the base attenuate to a narrowly winged petiole 1–12 cm. long. Buds erect just before anthesis. Sterile prolongation of ovary 1.5–8 cm. long. Hypanthium 1.5–3 mm. long, 3–4 mm. across at summit, subglabrous outside, with short matted trichomes inside near the base. Sepals 4.1–13 mm. long, 0.8–3 mm. wide, sometimes very minutely strigulose, reflexed separately. Petals often apiculate, 5–16 mm. long, 5–16 mm. wide. Filaments of the episepalous stamens 1.8–6.5 mm. long, those of the epipetalous ones 0.5–2.5 mm. long; anthers 0.9–2 mm. long. Style 4–8.5 (–11) mm. long, glabrous or sparsely pubescent near the base; stigma 1–2 mm. in diameter, usually surrounded by the longer anthers at anthesis, but very rarely held above them. Capsule 11–28 mm. long, 5–8 mm. in diameter, 4-angled with flat walls, these thick and smooth and scarcely distended by the seeds, rarely with a pedicel up to 1 cm. long, becoming blackened and persistent on the plants for one or more years after shedding seeds. Seeds oblong, uniform tan to light brown, 1.3–1.9 mm. long, 0.6–1 mm. thick, coarsely pitted, the pits in ca. 25 parallel rows. Gametic chromosome number, $n=7$. Self-compatible but often outcrossed.

TYPE: Moist ground, Quamash Flats (Squamash Flats), on Weippe (Oyipe) Prairie, Shoshone County, Idaho, 14 June 1806, *M. Lewis* (PH). See Coues, Proc. Acad. Nat. Sci. Philad. 1898: 302. 1898. Locality incorrectly given by Pursh as "the banks of the Missouri," to which he credited many of the species from the Lewis and Clark Expedition even when the labels indicated other, more specific data (letter from F. W. Pennell to P. A. Munz, Feb. 17, 1928, filed at POM). See also Torrey & Gray, Fl. N. Amer. 1: 507. 1840; Raven,

Brittonia 16: 283. 1964, as to the application of this name to this species.

DISTRIBUTION (Figure 21): Wet, often clayey meadows, sometimes growing in deep grass, from Yakima, Kittitas, Chelan, Lincoln, and Spokane Counties, Washington, and Phillips County, Montana (Lake Bowdoin, *Blankinship* in 1903, MONT), south through Sheridan and Fremont Counties, Wyoming, to Routt County, Colorado; Summit Duchesne, and Sanpete Counties, Utah; White Pine, northern Nye, and Douglas Counties, Nevada; and in California east of the Cascade axis to the vicinity of Bodie, Mono County, and again on the Kern Plateau, Tulare County; 1,500–8,600 ft. alt.

Vouchers for chromosome number, $n=7$ (no structural heterozygosity observed; 4 individuals, 4 populations):

U.S.: CALIFORNIA: MONO CO.: 4.4 mi. NW. of Bridgeport, R18548. IDAHO: ADAMS CO.: 3 mi. W. of Big Payette Lake, R18508. VALLEY CO.: 2 mi. S. of McCall, R18510. OREGON: LAKE CO.: Hart Mountain Antelope Refuge Headquarters, R18430.

Individuals of the two populations of *Camissonia subacaulis* tested by pollen-tube growth have been found to be self-compatible and facultatively self-pollinating. In the first Idaho population mentioned above 16 individuals were tested, and 17 were tested in the California population. Pollinators were extremely rare at both localities, and the flowers were more or less hidden from view at the base of the rosette. In a few populations (such as *Hitchcock & Muhlick* 14048, DS, POM, Valley County, Idaho) the stigmas seem to be held above the anthers at anthesis, and some of the populations of this species might prove to consist of self-incompatible individuals. *Camissonia subacaulis* has been found growing sympatrically with *C. tanacetifolia* subsp. *tanacetifolia* and very probably occurs sympatrically with *C. breviflora* as well. This species appears to have no near relatives. An earlier approximate report of the chromosome number of this species was made by Johansen (Amer. Journ. Bot. 16: 597: 1929), but without any citation of voucher or locality.

22. Camissonia tanacetifolia (Torr. & Gray) Raven, Brittonia 16: 283. 1964.

Acaulescent perennial from a woody, deep taproot from which numerous slender branches arise in age to produce additional rosettes. Leaves very narrowly elliptic, 6.5–32 cm. long, 0.7–3.3 cm. wide, more or less densely short-pilose, or the trichomes appressed; deeply and irregularly pinnatifid, the apex acute to long acuminate, the base attenuate to narrowly cuneate to a petiole 1–8 cm. long. Buds erect just before anthesis. Sterile prolongation of ovary 1.4–5.5 cm. long. Hypanthium 4–6.5(–8.5) mm. long, 5–7(–11) mm. across at summit, short-pilose outside, soft-pilose in lower half within. Sepals 5.5–13 mm. long, 1.8–4.2 mm. wide, short-pilose, reflexed separately. Petals

(8–)10–23 mm. long, 7–15(–18) mm. wide. Filaments of the episepalous stamens 5.5–12 mm. long, those of the epipetalous ones 2.5–8 mm. long; anthers (2.3–) 2.8–3.5 mm. long. Style 9.5–20(–25) mm. long, pilose near the base; stigma depressed-globose, more or less 4-notched, 1.3–3.5 mm. in diameter, held well above the anthers at anthesis. Capsule 7–25 mm. long, 3–5 mm. thick, gradually attenuate to the sterile prolongation, subterete, the walls thick but evidently distended by the seeds, sessile, disintegrating irregularly the season after their formation. Seeds oblong, uniform tan to brown, 1.5–2 mm. long, 0.6–0.8 mm. thick, pitted in rows, with ca. 20 rows of pits. Gametic chromosome numbers, $n=7$, 14, 21. Self-incompatible, probably with some self-compatible populations.

DISTRIBUTION (Figure 24): Open clayey fields and moist slopes, sometimes by streams or lakes, Klickitat, Douglas, and Spokane Counties, Washington, and Owyhee, Ada, Elmore, Camas, and Blaine Counties, Idaho, south on the east side of the Sierra-Cascade axis to Elko, northernmost Nye, and Douglas Counties, Nevada, and the vicinity of Bodie and Conway Summit, Mono County, California. From about 1,300 ft. alt. in the north to 8,200 ft. in the south. Gregarious and often coloring large fields yellow when in bloom.

22a. Camissonia tanacetifolia subsp. **tanacetifolia.** FIGURES 11, 17, 23

Oenothera nuttallii Torr. & Gray, Fl. N. Amer. 1: 506. 1840; not Sweet 1830. Type: Said to be from "Plains in the Rocky Mountains, near Blackfoot River," which would put it in or near Caribou County, Idaho, 10–11 July 1834, *T. Nuttall* (isotype PH), at the type locality for the following species and far from any known locality for the present one; therefore, the locality as given is probably in error.

Oenothera tanacetifolia Torr. & Gray, Pac. R. R. Rept. 2: 121, *pl. 4*. 1854.

Taraxia longiflora Nutt. ex Howell, Fl. N.W. Amer. 231. 1891–1896.

Taraxia tanacetifolia (Torr. & Gray) Piper, Contr. U.S. Nat. Herb. 11: 405. 1906.

Taraxia tikurana A. Nels., Bot. Gaz. 54: 140. 1912. Lectotype: Tikura, Blaine Co., Idaho, 4,500 ft. elev., 22 July 1911, *A. Nelson & J. F. Macbride* 1302 (RM; isolectotypes, DS, GM, NMC, POM, US.)

Plants more or less densely pilose or the trichomes appressed; rarely more than 5 percent of the pollen with 4 pores. Gametic chromosome numbers, $n=7$, 14. Self-incompatible, probably with self-compatible populations.

TYPE: Vicinity of Pah-Rum Peak, Lake Range, Washoe County, Nevada, 18 June 1854, *E. G. Beckwith* 43 (GH, the specimen from which the illustration was prepared; isotype, NY). Type locality given as "On the higher parts of the Sierra Nevada" but the actual locality was reconstructed from Beckwith's account of the expedition (Pac. R.R. Rept. 2(1b): 1–70. 1854).

DISTRIBUTION (Figure 24): That of the species, but not found in and near Sierra Valley in Plumas and immediately adjacent portions of Lassen and Sierra Counties, California.

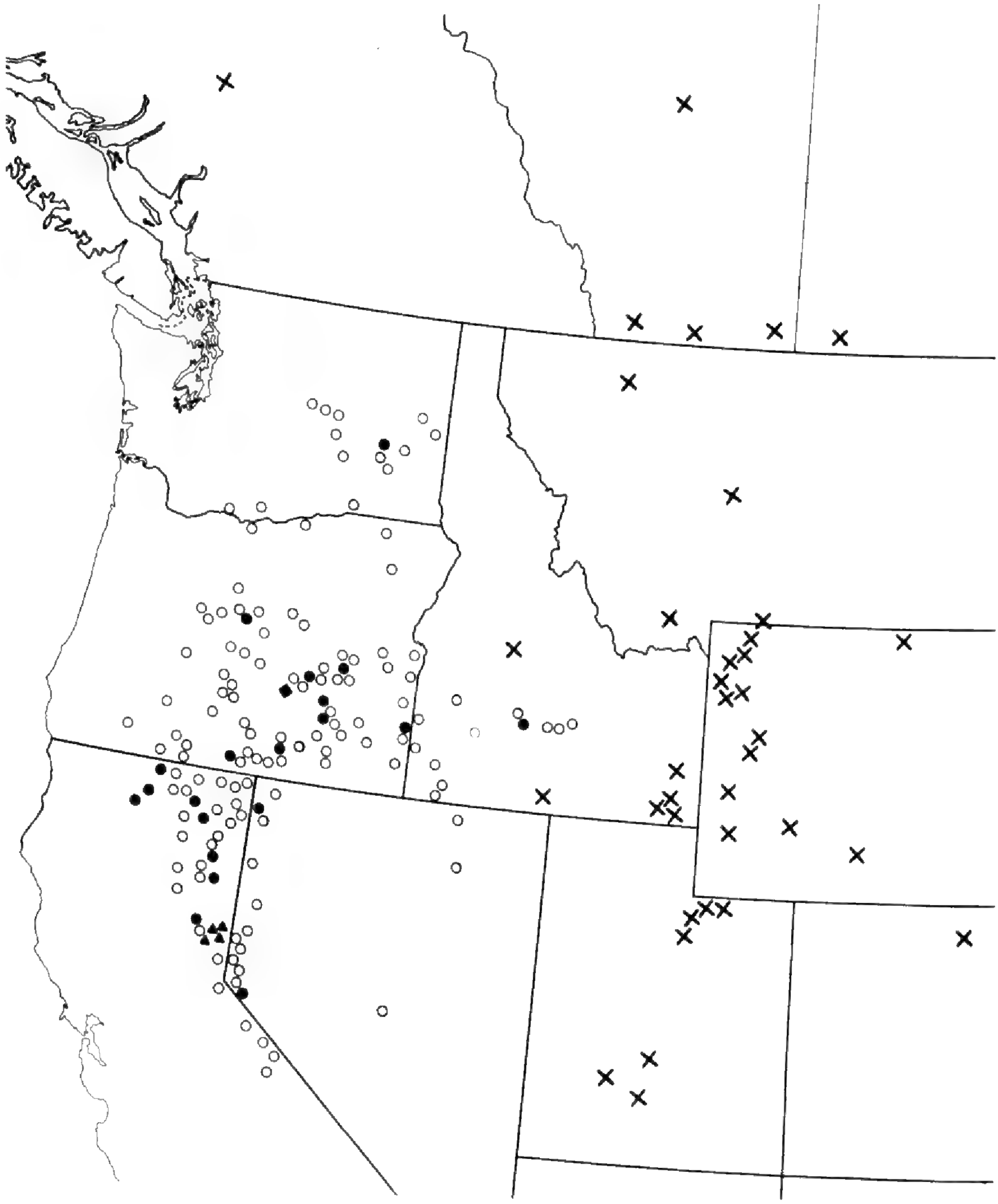


FIGURE 24.—Western United States and a portion of adjacent Canada, showing ranges of species of *Camissonia* sect. *Tetrapteron:* ○=*C. tanacetifolia* subsp. *tanacetifolia*, with ●=tetraploid chromosome counts ($n=14$) and ♦=the single diploid count ($n=7$); ▲=*C. tanacetifolia* subsp. *quadriperforata* (all hexaploid, $n=21$); ×= *C. breviflora.*

Voucher for chromosome number, $n=7$ (1 structurally homozygous individual):

U.S.: OREGON: HARNEY CO.: 0.6 mi. N. of Wagontire, R18432.

Vouchers for chromosome number, $n=14$ (with variable numbers of rings of 4 chromosomes in meiotic metaphase I, the maximum number of such rings observed in each case indicated in parentheses

following the collection number; other chromosomes present as bivalents; 25 individuals, 25 populations):

U.S.: California: lassen co.: U.S. Hwy. 395, 11.1 mi. N. of Litchfield, R18423 (3); 0.9 mi. N. of Ravendale, R18426; 11.6 mi. N. of Litchfield, R17875 (3); 0.5 mi. N. of Ravendale, R17876 (5). modoc co.: 13 mi. NW. of Canby, R17893; State Hwy. 139 at S. road to Lava Beds National Monument, R17896 (4). plumas co.: Middle Fork of Feather R. just N. of Mohawk, *Mosquin & Gillett* 5302 (3). siskiyou co.: Grass Lake, *Bates* 2436; 14 mi. S. of Macdoel, R17900; 4.4 mi. S. of Dorris, R17898. Idaho: camas co.: Near Camas Creek and State Hwy. 46, R18526 (5). elmore co.: 2.7 mi. N. of Mountain Home, R18523. owyhee co.: U.S. Hwy. 395, 9.3 mi. NE. of the Oregon line R19576. Nevada: douglas co.: U.S. Hwy. 395, 2.9 mi. N. of junction with State Hwy. 3, R18546; S. end of Double Spring Flat, R14267. washoe co.: 20 mi. E. of Cedarville (Calif.) on State Hwy. 8A, R17885 (3). Oregon: crook co.: N. road from Prineville to Big Summit Prairie, *Chambers & Lewis* 1934. harney co.: U.S. Hwy. 20, 7.4 mi. E. of junction with U.S. Hwy. 395, R18457; 8.4 mi. N. of Narrows, R18456; 23.2 mi. S. of Narrows, R18454 (4); U.S. Hwy. 20, 2.1 mi. W. of junction to Ft. Harney, *T. & L. Mosquin* 4345 (DAO). lake co.: 0.9 mi. E. of Hart Mountain Antelope Refuge Headquarters, R18341 (5); 4.1 mi. E. of Drew's Reservoir, W. of Lakeview, R18428. malheur co.: 6 mi. N. of Jordan Valley, R19583. Washington: adams co.: 4 mi. NE. of Ritzville, R18496.

Twelve individuals from the Washington population just cited appeared to be self-compatible, judging from pollen-tube growth in selfed, caged individuals. On the other hand, 25 plants of the first-mentioned Lake County, Oregon, population proved to be self incompatible, as did 17 individuals from the Douglas County, Nevada, population. *Andrena* (*Onagrandrena*) *raveni* Linsley & MacSwain is oligolectic on plants of the tribe Onagreae, and females of this species have been observed abundantly gathering pollen on *Camissonia tanacetifolia* subsp. *tanacetifolia* in a number of populations. Outcrossing is certainly the mode in *Camissonia tanacetifolia*, and the existence and distribution of self-compatible plants needs to be studied in greater detail.

From a chromosomal point of view, 25 of the 26 populations of this subspecies examined have been effectively autotetraploid, usually with 3 rings of 4 chromosomes in each diakinesis or metaphase I cell, but occasionally with up to 5 rings of 4. It is not known whether the diploid set of chromosomes duplicated twice in these plants is structurally homologous with that in the related diploid *C. breviflora*, but that species is autogamous and small-flowered, and cannot be identical with the ancestor of the self-incompatible, large-flowered, polyploid *C. tanacetifolia*. No other related diploid is known.

The single diploid strain of *C. tanacetifolia* subsp. *tancetifolia* was found during the course of an extensive survey of chromosome numbers throughout the range of this taxon (fig. 24). It is morphologically identical to the tetraploid plants that occur in the same area, and it could therefore be their diploid ancestor. In my opinion, how-

ever, it is at least equally probable that this single diploid population (perhaps no more than a single plant) is a polyhaploid derivative of the predominant tetraploid. The chromosomes of the tetraploid are like those of other tetraploids that have given rise occasionally to fertile polyhaploid (=diploid) derivatives (Raven & Thompson, Amer. Nat. 98: 251–252. 1964). Meiotic accidents that could lead to the formation of such a diploid derivative are known to occur sporadically in plants of this sort. I can think of no way to distinguish these two competing hypotheses concerning the origin of this diploid plant or population at present.

Camissonia tanacetifolia subsp. *tanacetifolia* has been found growing sympatrically with *C. subacaulis*. It is closely related to the autogamous, diploid *C. breviflora* but sharply distinct in flower size.

22b. Camissonia tanacetifolia subsp. **quadriperforata** Raven, subsp. nov.

A subsp. *tanacetifolia* differt: foliis villose incanis; plus quam 10 percentum pollinis grana plerumque quadripora; chromosomatum numero gametico, $n=21$.

TYPE: Common on flats with *Artemisia*, 6.2 miles north of Sierraville on road to Loyalton, Sierra County, California, 28 May 1963, *P. H. Raven* 18416 (DS 502795; isotypes RSA, US).

DISTRIBUTION (Figure 24): Common on more or less open clay flats, often with *Artemisia*, in Sierra Valley, Plumas County, and immediately adjacent portions of Lassen and Sierra Counties, California; 4,300–5,100 ft. alt.

Vouchers for chromosome number, $n=21$ (with many rings of 6 at diakinesis and meiotic metaphase I; 4 individuals, 4 populations): U.S.: CALIFORNIA: PLUMAS CO.: The type collection, cited above; 3.1 mi. W. of Vinton, R18419; 6.9 mi. S. of Vinton, R18417: ca. 2.5 mi. SE. of Beckwourth, ca. 5,000 ft., *Ornduff* 4347 (LA). SIERRA CO.: State Hwy. 49, 2.4 mi. WNW. of Sierraville, R18415.

ADDITIONAL SPECIMENS EXAMINED:

U.S.: CALIFORNIA: LASSEN CO.: Long Valley, sec. 34, T. 45 N., R. 17 E., 4,300 ft., *Sawyer* 219 (RSA, UC): Chat, 5,000 ft., *Hillman* in 1897 (POM), *Jones* in 1897 (POM): 3 mi. N. of Omira, *Howell* 11857 (CAS). PLUMAS CO.: Sierra Valley, *Bolander & Keller* in 1872 (NY), *Lemmon* 87 (GH), in 1873 (GH), *Hillman* in 1898 (POM); Portola, *Eastwood* 7051 (CAS); 1.7 mi. NE. Vinton, 5,000 ft., *Cantelow* in 1941 (CAS, RSA); 8 mi. N. of Chilcoot, 5,000 ft., *Munz* 11823 (COLO, NY, RSA, RM, SD, UT, WTU); Chilcoot, 4,995 ft., *Rose* 34411 (CAS, RM); 4¾ mi. SE. of Sugarloaf, 4,900 ft., *Sawyer* 90 (POM, RSA); along road to Beckwourth, from Calpine, Sierra Valley, ca. 4,800 ft., *Bacigalupi* 4282 (JEPS, RSA): Beckwith Pass, 4,800 ft., *Jepson* 7767 (DS, JEPS): near Beckwourth, 4,900 ft., *Howell* 30753 (CAS), 37769 (CAS). SIERRA CO.: Loyalton, *Clemens* in 1920 (CAS). WITHOUT DEFINITE LOCALITY: *Lemmon* in 1875 (POM), 104 (NY).

Camissonia tanacetifolia subsp. *quadriperforata* is narrowly distributed and can be recognized most easily by a characteristic directly

related to its hexaploid chromosome number: namely, the relatively high proportion of 4-pored pollen grains. Plants of this taxon are essentially identical in all other respects to those of subsp. *tanacetifolia* found in neighboring areas, although they do differ morphologically from a majority of the populations of subsp. *tanacetifolia* found in other areas. There is no known diploid population that could have combined with the tetraploid subsp. *tanacetifolia* to give rise to this hexaploid. In view of this and the local distribution of subsp. *quadriperforata*, its lack of morphological distinctness from adjacent tetraploid populations of the species, and the behavior of its chromosomes in meiosis, it seems likely that this hexaploid arose directly from the adjacent tetraploid populations by the functioning of an unreduced gamete. Probably the hexaploid originated recently and only once and has since spread to occupy its present area, which is less than 25 miles across at its broadest point. The habitat occupied is uniform and continuous. In order to understand how this postulated series of events could have occurred, however, it is necessary to assume that the hexaploid is physiologically superior to the tetraploid in its area, for it has apparently replaced the tetraploid where it does occur.

The nearest stations of hexaploid and tetraploid plants appear to be approximately 9 miles apart at present, with subsp. *tanacetifolia* at Graeagle (*Mason* 1037, DS, POM, UC) and subsp. *quadriperforata* to the east at Portola. Both of these stations are on the Middle Fork of the Feather River in Plumas County, California.

23. Camissonia breviflora (Torr. & Gray) Raven, Brittonia 16: 283. 1964.

FIGURES 12, 18, 22

Oenothera breviflora Torr. & Gray, Fl. N. Amer. 1: 506. 1840.

Taraxia breviflora (Torr. & Gray) Nutt. ex Small, Bull. Torrey Cl. 23: 185. 1896.

Similar to *C. tanacetifolia*. Plants densely clothed with appressed long trichomes. Leaves 1.7–10 cm. long, 0.35–3.3 cm. wide, the petiole 1.5–3 cm. long. Sterile prolongation of ovary 0.4–1.5 cm. long. Hypanthium 1.8–2 (–2.5) mm. long, 2.3–4 mm. across at the summit. Sepals 3.8–5 (–7.5) mm. long, 0.9–2.2 mm. wide. Petals 5.5–7 (–8) mm. long. 2.8–5 (–6) mm. wide. Filaments of the episepalous stamens 2.8–4 (–5) mm. long, those of the epipetalous ones 1.5–1.8 (–2) mm. long; anthers 0.9–1.3 mm. long. Style 3–6.5 mm. long; stigma globose, 1.1–1.6 mm. in diameter, surrounded by and receiving pollen directly from the anthers of the longer stamens at anthesis. Capsule 8–17 mm. long, 2–5 mm. thick. Seeds 1.5–1.8 mm. long, 0.7–0.9 mm. thick. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Near the Blackfoot River, in or near Caribou County, Idaho, 10–11 July 1834, *T. Nuttall* (GH; isotypes, BM, K, NY, PH).

DISTRIBUTION (Figure 24): Moist, often muddy or sandy flats, sometimes on lakeshores or in the dried beds of ponds in the vicinity

of Chilko Lake (Nemiah Trail, 4,500 ft., *Copley* 440, DAO), at ca. 51° N., 124° W. in central British Columbia; from the region of Drumheller, Alberta (Handhills Lake, 51°30′ N., 112°07′ W., *Macoun* 144, BM, GH, NY), and Loomis, southwestern Saskatchewan (*Hudson* 1966, DAO), south to Montana (Glacier, Cascade-Meagher, Park, and Madison Counties), Wyoming (Yellowstone National Park, Teton, Sublette, Sheridan, Sweetwater, and Lincoln Counties), Colorado (Larimer County: North Park, *Osterhout* 1036, RM), Idaho (Caribou, Bear Lake, Franklin, Custer, and Cassia Counties), and Utah (Summit, Wasatch, Sevier, Piute, and Garfield Counties, reaching its southern limit on the Aquarius Plateau); from 3,500 ft. (at its northern limits) to 10,000 ft. elevation, apparently always above 6,500 ft. in the United States, In south-central Idaho, populations of *C. breviflora* are found within 65 miles of populations of the related *C. tanacetifolia*, but the former is found in mountain meadows at approximately 8,000 ft. elevation, the latter on more or less alkaline flats from 3,000–4,500 ft. elevation. Records of *C. breviflora* from south and west of Cassia County, Idaho, are based on misidentifications of sometimes stunted specimens of *C. tanacetifolia*. One such erroneous record is that of Munz (Calif. Fl. 952. 1959), based on *Wheeler* 3744 (POM, NY, US) from the Warner Mountains of Modoc County, California; *Camissonia breviflora* is not known from any locality in or near California.

Voucher for chromosome number, $n=7$ (1 structurally homozygous individual):

U.S.: WYOMING: SWEETWATER CO.: Eden Valley Reservoir, ca. 6,600 ft., R19551.

Plants of the collection just cited were grown at Stanford for several years and found to be autogamous, shedding pollen directly on the stigma and setting full capsules even when protected from insects. It is presumed that *Camissonia breviflora*, which is relatively uniform morphologically, is an autogamous derivative of the diploid ancestor of *C. tanacetifolia*. These two species have been confused in the past, but are sharply distinct both morphologically and ecogeographically. *Camissonia breviflora* almost certainly occurs sympatrically with *C. subacaulis*.

24. Camissonia graciliflora (Hook. & Arn.) Raven, Brittonia 16: 283. 1964.

Oenothera graciliflora Hook. & Arn., Bot. Beechey Voy. 341. 1838.

Taraxia graciliflora (Hook. & Arn.) Raimann, *in* Engl. & Prantl, Natürl. Pflanzenfam. III. 7: 216. 1893.

Annual, acaulescent or less commonly with short ascending lateral branches up to 2.5 cm. long. Leaves linear to very narrowly lanceolate, 1–9.8 cm. long, 0.1–0.9 cm. wide, more or less densely pilose, entire or very sparsely serrulate, sessile, dilated at the base, the margins of the basal portion membranous. Buds nodding before anthesis but flowers

erect. Sterile prolongation of ovary 0.6–4.5 cm. long. Hypanthium 1.6–3.2 mm. long, 1.8–5 mm. across at the summit, pilose outside, more sparsely so inside, especially near the base. Sepals 4.5–8 mm. long, 1.2–2.9 mm. wide, pilose, reflexed in pairs. Petals 5–18 mm. long, 4.8–13 mm. wide. Filaments of the episepalous stamens 1.8–3.2 mm. long, those of the epipetalous ones 0.8–1.6 mm. long. Style 3–5.5 mm. long, short-pubescent near the base; stigma 1–1.6 mm. in diameter, surrounded by the anthers of the longer stamens at anthesis. Capsule 4–8 mm. long, 2.6–4.8 mm thick, sharply 4-angled and with a pointed wing near the center top of each valve, thick-walled (almost woody) and very tardily dehiscent, splitting for only about a third of its height. Seeds obovoid, tan mottled with brown, finely papillose, 1.2–2 mm. long, 1–1.2 mm. thick. Gametic chromosome number, $n=7$.

TYPE: California, 1833, *D. Douglas* (K; isotypes, BM, GH, NY).

DISTRIBUTION (Figure 25): Colonial on open or brushy slopes, often in clayey soil, from near sea level to about 2,500 ft. elevation; from Josephine County, Oregon, south in the Coast Ranges and foothills of the Sierra Nevada to Ventura and Los Angeles Counties, California; San Ysabel, San Diego County, *Henshaw* in 1893 (NY); red clay soil in once-cultivated field, Rancho Aguajito, 300 m., 29°59′N., 115°15′W., Baja California, *Raven et al.* 12675 (UC; the only known occurrence of the section in Mexico). Usually away from the coast, but collected both in Marin County (Mt. Tamalpais (*Wood* in 1915, CAS) and in San Francisco (*Cannon* in 1896, CAS), California. Once collected as an introduced plant in a dry, weedy field, St. George, Rockland County, New York, 20 July 1933, *Moldenke* 8008 (NY).

Voucher for chromosome number, $n=7$ (1 structurally homozygous individual):

U.S.: CALIFORNIA: MONTEREY CO.: Jolon, *Breedlove* 4279.

Camissonia graciliflora has been collected growing sympatrically with the very closely related *C. palmeri* (1 mile west of Pearblossom, Los Angeles County, California, *Mosquin* 3264, DAO; 3260, *C. palmeri*) and with *C. ovata*. It is self-compatible and facultatively self-pollinated, as shown by pollen-tube growth in three plants of R18153, Monterey County, California, that were caged in the field, and eight plants of R18177, San Luis Obispo County, California, that were grown in the experimental garden at Stanford. This species is probably not regularly outcrossed, judging from observations made at Jolon, Monterey County, California, on 31 March 1963 (Raven, MS.). With *C. palmeri* it forms a very distinctive group in the section, marked by annual habit, distinctive capsule morphology, obovoid seeds, nodding buds, and sepals reflexing in pairs; nonetheless, these two species so closely resemble the perennial members of the section in details of floral morphology (such as the sterile projection on the ovary, and the

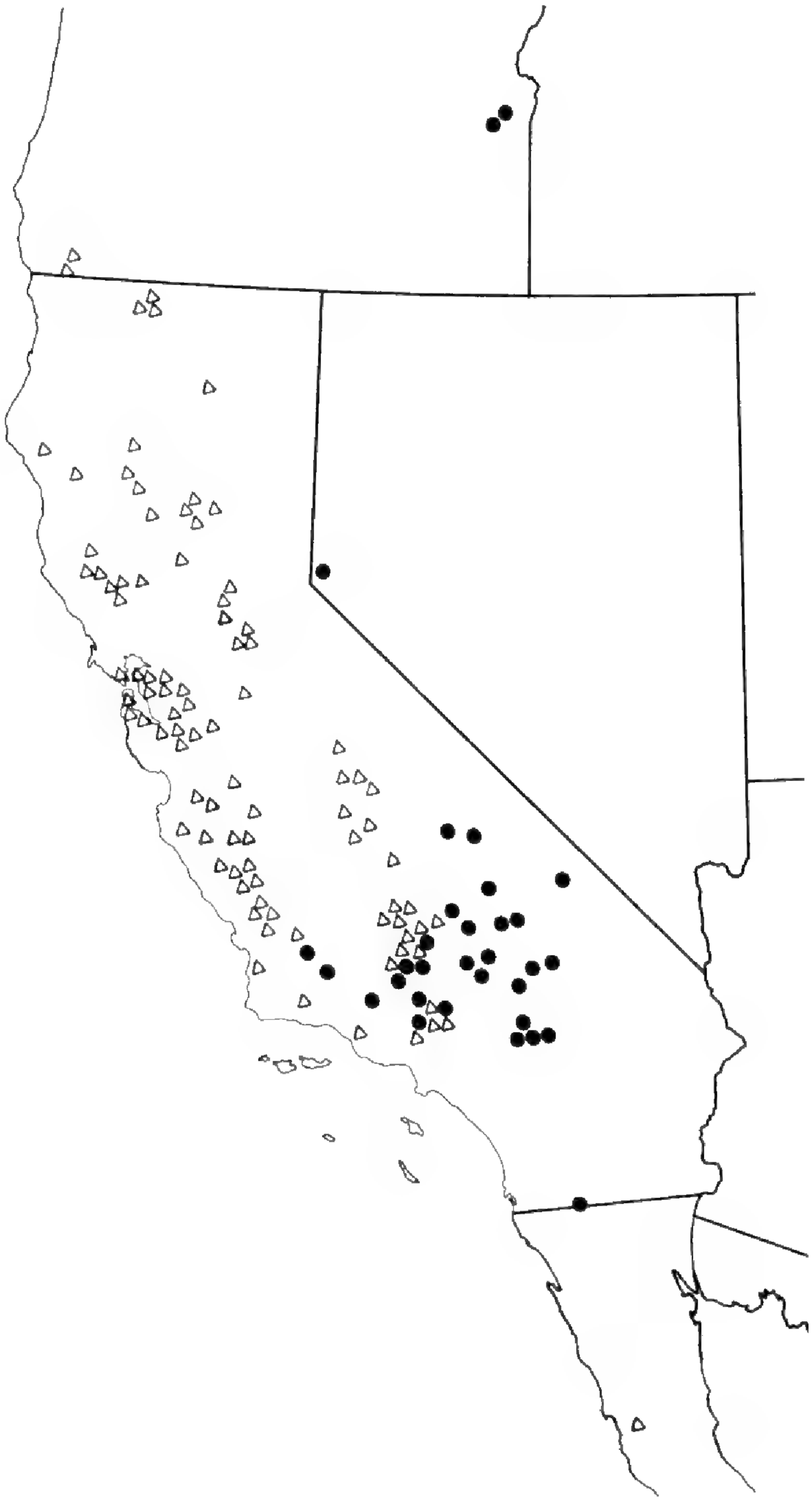


FIGURE 25.—Portion of the western United States and adjacent Mexico, showing the ranges of species of *Camissonia* sect. *Tetrapteron:* △=*C. graciliflora;* ●=*C. palmeri.*

fleshy ring closing the bottom of the hypanthium), that I believe they are best kept together in a single section.

25. Camissonia palmeri (S. Wats.) Raven, Brittonia 16: 283. 1964. FIGURES 14, 20

Oenothera palmeri S. Wats., Proc. Amer. Acad. 12: 251. 1877.

Taraxia palmeri (S. Wats.) Small, Bull. Torrey Cl. 23: 184. 1896.

Similar to *C. graciliflora.* Branches swollen, to 5 mm. thick, with conspicuously exfoliating white rhytidome. Leaves narrowly oblanceolate, 1.5–5.5 cm. long, 0.18–0.6 cm. wide, strigose, rarely with a few spreading trichomes near the base, sparsely but evenly serrulate.

Sterile projection of ovary 0.55–1.2 cm. long. Hypanthium 0.8–1.3 mm. long, 0.8–1.2 mm. across at the summit, strigose outside, glabrous within. Sepals 1.6–2.3 mm. long, ca. 1 mm. wide, strigose. Petals 2–3.5 mm. long, 1.8–4 mm. wide. Filaments of the episepalous stamens 0.8–1 mm. long, those of the epipetalous ones ca. 0.2 mm. long. Style 1–2.2 mm. long, glabrous; stigma 0.3–0.6 mm. in diameter, surrounded by the anthers of the long and short stamens, both of which shed pollen directly onto it at anthesis. Capsule 5–7 mm. long, 4.5–7 mm. thick, with much more prominent points than in *C. graciliflora*. Seeds narrowly obovoid. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Arizona, 1876, *E. Palmer* 597 (GH), perhaps from the Colorado River valley. The only known collection from this State, where the occurrence of the species needs to be confirmed; cf. McVaugh & Kearney, Amer. Midl. Nat. 29: 775–778. 1943.

DISTRIBUTION (Figure 25): Deserty flats, often under sagebrush, 2,000–4,650 ft. elevation, along the Malheur River near Vale, Malheur County, Oregon; 20 miles north of Winnemucca, Humboldt County. (*Ripley & Barneby* 4568, NY) and Empire City, Ormsby County. (*M. E. Jones* in 1882, GH, POM, UC), Nevada; in California fairly common from southern Inyo County, to the southwestern borders of the Mojave Desert, west to the vicinity of Tejon Pass and southeastern San Luis Obispo County in the inner South Coast Ranges, and also east of Jacumba on road to Mountain Springs, San Diego County (*Eastwood* 9553, CAS). May also occur in Arizona (cf. the type collection).

Voucher for chromosome count, $n=7$ (1 structurally homozygous individual):

U.S.: CALIFORNIA: SAN LUIS OBISPO CO.: Temblor Grade, Elkhorn Valley Road, south of Crocker Grade, *Lewis & Thompson* 1635 (LA, RSA).

As noted under that species, *Camissonia palmeri* has been collected growing sympatrically with *C. graciliflora*. Its floral structure provides unequivocal evidence of its autogamy. Indeed, some plants of both *C. palmeri* and *C. graciliflora* become cleistogamous under certain circumstances, these conditions being poorly understood. Such cleistogamous individuals, or other plants lacking flowers, can be determined only with difficulty. Plants of both species remain rooted in the ground long after they have died, the capsules shedding the seeds slowly after the first autumn rains.

Section V. *Holostigma*

Agassizia Spach, Hist. Vég. Phan. 4: 347. 1835; not Chavannes 1830.
Holostigma Spach, Nouv. Ann. Mus. Paris III. 4: 332. 1835.
Oenothera subg. *Sphaerostigma* sensu Munz, Bot. Gaz. 85: 234. 1928; pro parte.
Oenothera sect. *Holostigma* (Spach) Munz, N. Amer. Fl. II. 5: 159. 1965.

Perennials or annuals, the plants caulescent but with a well-developed basal rosette, flowering from the base. Inflorescence nodding at anthesis, becoming erect in fruit. Flowers opening near sunrise. Ovary lacking a sterile projection. Sepals reflexed separately or in pairs. Petals yellow, often with one to several red dots near the base, fading reddish, with no contrasting pattern visible in ultraviolet light. Stamens, style, and inside of hypanthium yellow, the stigma yellow or greenish yellow. Capsule regularly loculicidal, often contorted, not torulose, with a prominent brown rib down the center of each valve, the seeds in one row in each locule. Seeds with a scar at the micropylar end and a poorly developed pellucid chalazal crest, dull, brownish black, minutely lacunose in rows, narrowly obovoid.

TYPE SPECIES: *Camissonia cheiranthifolia* (Hornem. ex Spreng.) Raimann.

DISTRIBUTION: Brushy or open slopes and flats throughout cismontane California and the northern half of Baja California, with two species ranging across the deserts from southern Inyo County, California, and Esmeralda County, Nevada, across southern Arizona to the vicinity of Tucson, and one species ranging north along the coast to Coos Bay, Curry County, Oregon. Not known from, but possibly to be expected in, Sonora.

In all species of sect. *Holostigma*, the leaves of the basal rosette and the first formed capsules are more densely pubescent than those formed later. The leaves of the basal rosette tend to be broadest near the middle, and those of the stems and inflorescence tend to be broadest near the base and often subsessile or with shorter petioles. The first formed flowers are small, the largest ones are formed later and decrease markedly in size as the flowering season comes to an end. For all of these reasons it is especially necessary to deal with comparable stages when evaluating material of some of the critical species in this section.

The group of species comprising sect. *Holostigma* has always been a particularly difficult one taxonomically, both for the reasons just mentioned and because of their reticulate, polyploid pattern of evolution (see Appendix). In the treatment presented here, I have recognized 14 species, 3 of which are divided into 2 subspecies each. Of these 14 species, 9, including all of the polytypic ones, are diploid; 2 are tetraploid; and 3 are hexaploid.

All 9 diploids are relatively distinct from one another, although there is some intergradation between them. Both self-incompatible entities in the section are diploid: the ditypic, perennial *C. cheiranthifolia*, a species of the coastal strand from Coos Bay, Oregon, south to northern Baja California (partly consisting of self-compatible individuals), and the mostly annual *C. bistorta* that intergrades broadly

with *C. cheiranthifolia* along the coast of southern California. Of the remaining seven diploids, *C. guadalupensis* of San Clemente and Guadalupe Islands, *C. ignota* of southern California and scattered localities northward, and *C. proavita* of coastal northern Baja California are extremely distinct and do not appear to have contributed to the origin of any of the polyploid species.

The difficulty lies with the remaining four diploid species and their polyploid derivatives. *Camissonia lewisii*, found along the coast of southern California and the northern half of Baja California, may have been derived more or less directly from coastal populations of *C. bistorta*. In northern and central California and also extending into the main area of the group in southern California, *C. micrantha* is largely a species of sandy beaches, washes, and flats at relatively low elevations, whereas *C. hirtella* is a species of cleared brushy slopes and chaparral margins away from the coast. Although these two diploids are modally extremely distinct, they have apparently combined to produce a tetraploid, *C. intermedia*, which bridges the morphological and ecological gap between them and contributes materially to the taxonomic difficulties of the group. *Camissonia pallida*, a diploid with a very wide range in the deserts of southern California and adjacent Nevada, western and southern Arizona, and northeastern Baja California, is very closely related to *C. hirtella* and at times difficult to distinguish from it, although the species come into contact only at the margins of their ranges. Given this pattern of variation, it is not at all surprising that *C. confusa*, the probable allotetraploid between *Camissonia hirtella* and *C. pallida*, should compound the taxonomic problems of separating its two diploid ancestors and be difficult to recognize when compared with certain populations of the diploids.

Although *Camissonia confusa*, the rarer of the two tetraploids, does not appear to have contributed to the origin of any hexaploid species, *C. intermedia* has rather obviously done so. In Monterey and San Luis Obispo Counties, California, north of the main area of the section, *C. intermedia* appears to have combined with each of its parents, *C. hirtella* and *C. micrantha*, to have given rise to the local hexaploids *C. luciae* and *C. hardhamiae*, respectively. In Baja California, *C. intermedia* has evidently combined with *C. lewisii* to give rise to the hexaploid *C. robusta*.

With a reticulate pattern of variation of this sort, it is no wonder that taxonomic treatments accorded the group have varied widely, particularly in the absence of knowledge about chromosome number. Although there has been some variation in the number of species and varieties recognized, the perennial *C. cheiranthifolia* and the annual, self-incompatible *C. bistorta* generally have been recognized as distinct from the remainder of the group by virtue of their large flowers

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and long styles. The same is largely true of *C. guadalupensis*, described in 1876 but excessively rare in collections until the past five years. Most of the difficulty then has concerned the remaining species of the section, usually treated collectively as *Oenothera micrantha*.

How have different authors treated the *Oenothera micrantha* complex? E. L. Greene in 1891 subdivided this group into the more or less prostrate or trailing coastal *Oenothera micrantha*, which he allied to *Oenothera bistorta* of southern California, and the erect plant of the interior with broader leaves that he called *Oenothera hirtella*. Greene was the first author who had seen many populations in nature to deal with this group. In 1905, LeRoy Abrams realized the distinctiveness of the densely strigose desert populations, which he described as *Oenothera pallida*. Later the same year Aven Nelson, working largely with herbarium material, treated some material of both species that had been described as varieties of his *Sphaerostigma micranthum*, but also recognized *Sphaerostigma hirtellum* and described another species based on material of the same diploid taxon as *S. arenicola*. Nelson was evidently puzzled by the striking changes in plants of this group that occur with increasing maturity and had no acquaintance with them in the field; his work cannot be regarded as a forward step.

In 1907 appeared what were clearly the most perceptive remarks on the plants of this section written without knowledge of chromosome numbers. This paper was entitled "Notes on *Sphaerostigma*," by Anstruther Davidson, an enthusiastic amateur botanist of southern California. From his excellent vantage point Davidson was able to present a remarkably accurate picture of the entities represented in the group. He recognized as species *S. pallidum*, *S. hirtellum* ("a good and quite distinct species, and not a merely hirsute variety of *micranthum* as some have supposed"), and *S. micranthum*, and also described *S. hallii*, here regarded as a subspecies of *Camissonia pallida*. Davidson's remarks about the pattern of variation in his *S. micranthum* are remarkable and deserve to be quoted at some length (Muhlenbergia 3: 107. 1907):

> The typical plant of this species is, I presume, the ordinary moderately hirsute, semi-prostrate form found from San Francisco southward. In the coast region round Los Angeles there are two well marked forms. One, the congesta form, has very congested foliage, with the leaves larger and more hirsute, and with very small flowers; the other, the macrocarpa form, with the same foliage, has the short stout capsule of *bistorta*. The latter is the rarer form, examples of which are found from Los Angeles, San Diego, and Lower Califormia. A typical interior form is found in Parish's collections from San Bernardino county, and is frequently met with in other interior valleys. It is to the eye quite smooth in all its parts.

In retrospect, it is obvious that Davidson was quite correct about the typical form of the species, which is here recognized as *Camissonia*

micrantha; this also includes his "congesta" form. Davidson's "macrocarpa" form is obviously the species described 60 years later in the present revision as *C. lewisii*; and his "typical interior form" is the plant described by Jepson in 1925 as a variety of *Oenothera micrantha* and here regarded as a distinct species *Camissonia ignota*. In other words, Davidson recognized and quite accurately described all seven diploids with which he was familiar; it is probable that he saw no material of *C. proavita* or *C. gudalupensis*. The relatively few polyploid populations that he encountered were presumbly referred to one of the diploids, depending on their morphological relationships.

No subsequent author gained quite as clear a picture of the major patterns of variation in the group, possibly because of an increasing awareness of the way in which the polyploids recombined the characteristics of what otherwise would have been distinctive diploid races.

In 1928, P. A. Munz published his comprehensive review of the section. His concept of this complex was based on a comprehensive species, *Oenothera hirta* (=*Camissonia micrantha*), with four varieties corresponding broadly to the diploids *Camissonia micrantha*, *C. hirtella*, *C. ignota*, and *C. pallida*. Dr. Munz did not realize the distinctiveness of *C. lewisii* and *C. proavita* and had very little material of the latter upon which to base any judgment. Again the polyploids were redistributed among the diploid taxa they most closely resembled.

In 1964, I outlined the limits of sect. *Holostigma* accepted here and made new combinations at the specific level for the available names in the group (Brittonia 16: 276–288). This led Dr. Munz to accept his earlier varieties as species (Fl. N. Amer. II. 5: 159–163. 1965). He was unable to list *C. lewisii*, *C. proavita*, and the five polyploid species, as no earlier names were available for these entities.

The present study of *Camissonia* sect. *Holostigma* is clearly not a definitive one, and much work remains to be done. On the other hand, it represents 10 years of intensive fieldwork, cultivation of the plants in the experimental garden, and the determination of the chromosome numbers of 389 individuals from 335 populations (see Appendix). I believe that the taxonomy presented here leads to a clearer picture of the pattern of variation in the section than anything published previously, and I have had much more material to draw on than any earlier worker concerned with the group. Lines within and between the nine diploid species appear clearly drawn, but the nature and derivation of both tetraploids need to be investigated in much greater detail, preferably by the techniques of experimental hybridization. The delimitation of the three hexaploids seems clearer, but the same sort of work could profitably be done here also. At any rate, it is hoped that the present taxonomic synopsis offers a sound basis for such studies. As pointed out in the Appendix, the group appears to

have several cytogenetic peculiarities which should make a further investigation of the evolutionary patterns in it of more than usual interest.

26. Camissonia cheiranthifolia (Hornem. ex Spreng.) Raimann, *in* Engl. & Prantl, Natürl. Pflanzenfam. III. 7: 217. 1893.

Oenothera spiralis f. *arcuata* H. Lév., Monogr. Onoth. 222. 1905. Léveillé says simply "Fruit simplement arque—falque" and this cannot be placed with either of the two subspecies in the absence of authentic material.

Oenothera spiralis f. *clypeata* H. Lév., Monogr. Onoth. 222. 1905. Léveillé says "Feuilles *scutiformes*, sessiles, comme mucronees au sommet"; to assign this name to either subspecies in the absence of authentic material would be a guess.

Sphaerostigma spirale var. *clypeatum* (H. Lév.) A. Nels., Bot. Gaz. 40: 60. 1905.

Short-lived perennial, usually flowering the first year, with a circle of prostrate, decumbent, or more or less ascending stems radiating from a central rosette which withers in age, the stems to 0.6 (–1.3) m. long, ultimately somewhat woody and developing a conspicuously exfoliating reddish brown (less commonly whitish) rhytidome. Plants more or less densely strigose pubescent on all parts, rarely glabrous. Leaves narrowly ovate, 0.5–5 cm. long, 0.25–2.2 cm. wide, sparsely and weakly serrulate, the apex acute, the base cuneate to cordate or (in the basal rosette) attenuate; petioles to 2.5 cm. long in the basal rosette, 0–10 mm. long on the branches. Inflorescence with two types of trichomes, short-erect and long-villous. Hypanthium 2.1–8.5 mm. long, 1.5–5 mm. across at the summit, glabrous within. Sepals 4–11.5 mm. long, 1.3–3.4 mm. wide, reflexed in pairs. Petals 6–20 mm. long, 5–22 mm. wide, often red-dotted near the base. Filaments of the episepalous stamens 2.8–8 mm. long, those of the epipetalous ones 1.5–6 mm. long; anthers 1.3–3 mm. long. Style 6–23 mm. long, glabrous; stigma 0.4–1.5 mm. in diameter, surrounded by or held above the anthers at anthesis. Capsule 1–2.5 cm. long, ca. 2–2.5 mm. thick, quadrangular in transection, often curled in one or two spirals. Seeds 1.2–1.3 mm. long, 0.5–0.7 mm. thick. Gametic chromosome number, $n=7$. Self-incompatible, self-compatible but outcrossing, and autogamous races known.

Distribution (Figure 30): Sandy slopes and flats along the immediate coast and on islands from Coos Bay, Curry County, Oregon, to the vicinity of San Quintín, Baja California; also known from the east shore of San Francisco Bay and locally on sand dunes along the lower Sacramento River, California. Near sea level to several hundred feet elevation.

Although some 35 miles separate the southern limit of subsp. *cheiranthifolia*, at Point Conception, from the northern limit of subsp. *suffruticosa*, just above Goleta, both of the subspecies occur on San Nicolas Island. Here, as on the other Channel Islands where the

species occurs, subsp. *cheiranthifolia* is common and has been collected a number of times. On 24 April 1966, I found a small colony of about 40 plants of subsp. *suffruticosa* on the open dunes ca. 1 mile east-southeast of Seal Beach, at the northwest end of San Nicolas Island (my no. 20761, collected with H. J. Thompson). The colony was surrounded by about 15 intermediates and located near a road in a much larger population of subsp. *cheiranthifolia*. It is possible that subsp. *suffruticosa* was introduced on the island, but it was collected as early as 1901 (*Trask* 45, GH, NY), so it more likely reached the island by natural means. The population I studied presumably consists of self-compatible plants, although the stigma was held well above the anthers as usual in this subspecies.

Experimental hybrids were made between plants of subsp. *suffruticosa* from Point Dume, Los Angeles County, California, and subsp. *cheiranthifolia* from Jalama Beach, Santa Barbara County, California. Both parental strains had 7 pairs of chromosomes at meiotic metaphase I, and both consisted of self-compatible plants. The F_1 hybrids (Raven 17746, 17747, 17934) were intermediate between the parents morphologically, self-compatible, and fully fertile, although the stigma was held above the anthers as in the subsp. *suffruticosa* parent. Reciprocal hybrids were indistinguishable, and one hybrid made in each direction was examined cytologically and found to form 7 pairs at meiosis, indicating a lack of structural differences. In terms of pollen stainability, three plants with subsp. *suffruticosa* as the pistillate parent had, respectively, 93, 80, and 88 percent stainable pollen (based on samples of 100 grains in cotton blue in lactophenol), and five with subsp. *cheiranthifolia* as the pistillate parent had, respectively, 66, 72, 58, 53, and 77 percent stainable pollen. Both parents had consistently more than 95 percent stainable pollen, thus indicating a definite, but limited, reduction in fertility in the F_1 hybrids apparently not associated with chromosomal differentiation between the parental strains.

26a. Camissonia cheiranthifolia subsp. **suffruticosa** (S. Wats.) Raven, Brittonia 16: 284. 1964. FIGURES 26, 27

Oenothera viridescens Hook., Fl. Bor. Amer. 1: 214. 1833. Type: From Santa Barbara, Santa Barbara Co., Calif., or San Diego, San Diego Co., Calif., November or December 1793, *A. Menzies* (K).

Sphaerostigma viridescens (Hook.) Walp., Rep. 2: 77. 1843.

Oenothera cheiranthifolia var. *sufflruticosa* S. Wats., Proc. Amer. Acad. 8: 592 1873.

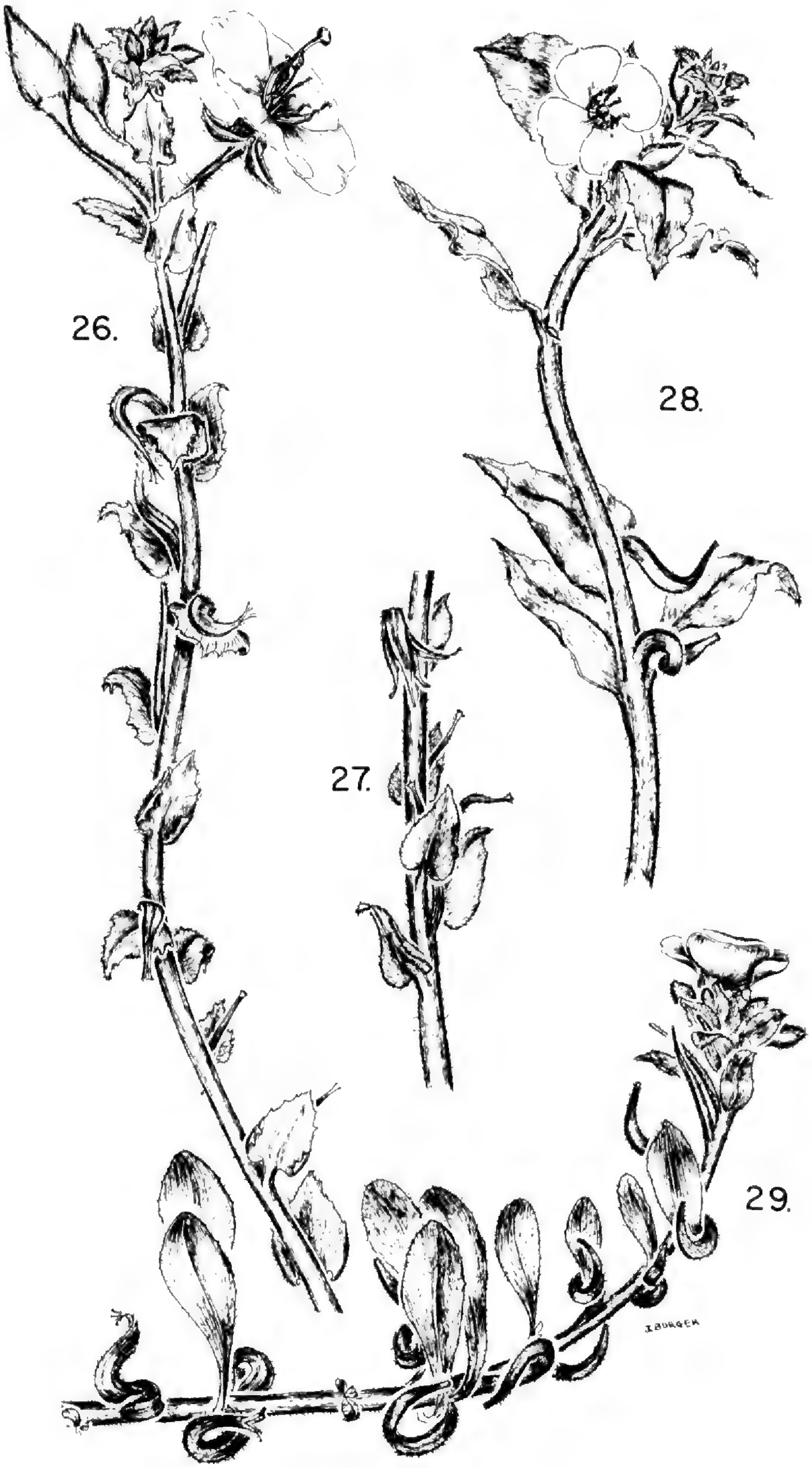
"*Oenothera virescens* Hook.," Greene, Fl. Francisc. 214. 1891.

Sphaerostigma spirale var. *viridescens* (Hook.) A. Nels., Bot. Gaz. 40: 60. 1905.

Oenothera spiralis f. *viridescens* (Hook.) H. Lév., Monogr. Onoth. 222. 1905.

Oenothera spiralis var. *linearis* Jeps., Man. Fl. Pl. Calif. 684. 1925. Type: Sunnyside, San Diego Co., Calif., April 1903, *H. M. Ha* 3908 (UC).

Oenothera spiralis var. *viridescens* (Hook.) Jeps., Man. Fl. Pl. Calif. 684. 1925.



FIGURES 26–29.—*Camissonia cheiranthifolia*, × 1: 26–27, *C. cheiranthifolia* subsp. *suffruticosa* (*Gregory* 468, DS): 26, Flowering branch; 27, portion of fruiting branch. 28–29, *C. cheiranthifolia* subsp. *cheiranthifolia*, flowering branches: 28, *Raven* 20825, DS; 29, *Randall* 220, DS.

Often bushy, the branches ascending and the plants quite woody; pubescence often dense and silvery, particularly in the summer and fall. Hypanthium 5–8.5 mm. long, 3–5 mm. across at the summit. Sepals 6–11.5 mm. long, 2.4–3.4 mm. wide. Petals (10–) 12–20 mm. long, 14–22 mm. wide, usually with one or two red dots at the base. Filaments of the episepalous stamens 5–8 mm. long, those of the epipetalous ones 3–6 mm. long. Anthers 2.2–3 mm. long. Style 13–23 mm. long; stigma held well above the anthers at anthesis. Gametic chromosome number, $n=7$. Outcrossing, with self-incompatible and self-compatible populations known.

LECTOTYPE: Santa Barbara, Santa Barbara County, California, *Brewer* 307 (GH). This appears to be the only specimen in the Gray Herbarium annotated with this name by Watson. Considering this, and the fact that it is from a definite locality, it appears to be a better choice of lectotype than the first-listed specimen assumed by Munz (Bot. Gaz. 85: 269. 1928) to be the type.

DISTRIBUTION (Figure 30): Sand dunes and beaches along the immediate coast, from Deveraux Dunes just west of Goleta, Santa Barbara County, California, to 6 miles south of San Quintín, Baja California (*Ballou & Canby* in 1925, C, F, POM, UC); San Nicolas Island, Ventura County, California (see below); San Martín Island, Baja California. From near sea level to several hundred feet elevation.

The chromosome number has been determined from 8 individuals from 7 different populations scattered throughout the range of this entity (see Appendix). Populations from 5.5 miles southeast of Point Mugu, Ventura County, California (R20161—6 plants tested for growth of pollen tubes), Point Dume (see below), and Playa del Rey (Kyhos 65–47, 1 plant grown at Stanford), Los Angeles County, California, consisted of self-compatible plants, which were however outcrossing, with the stigma elevated well above the stamens at anthesis and not contacting them even when the flowers closed. On the other hand, populations from farther south, in San Diego County, California, consisted of self-incompatible individuals: Del Mar Beach, R20167 (11 plants tested for pollen-tube growth); DeAnza Cove, Mission Bay, *Wedberg* (15 plants grown at Stanford as R66–224). *Andrena* (*Onagrandrena*) *oenotherae* Timb. was an abundant visitor to the flowers of this subspecies at all localities investigated, extending from the northern limit to south of Ensenada, Baja California; this large, black, oligolectic bee doubtless is a very important agent promoting outcrossing in this subpecies. *Andrena* (*Diandrena*) *parachalybea* Viereck, a somewhat smaller oligolectic bee, is locally frequent as an early morning visitor to the present subspecies also.

It appears likely that populations very similar to the self-incompatible ones presently referred to *Camissonia cheiranthifolia* subsp.

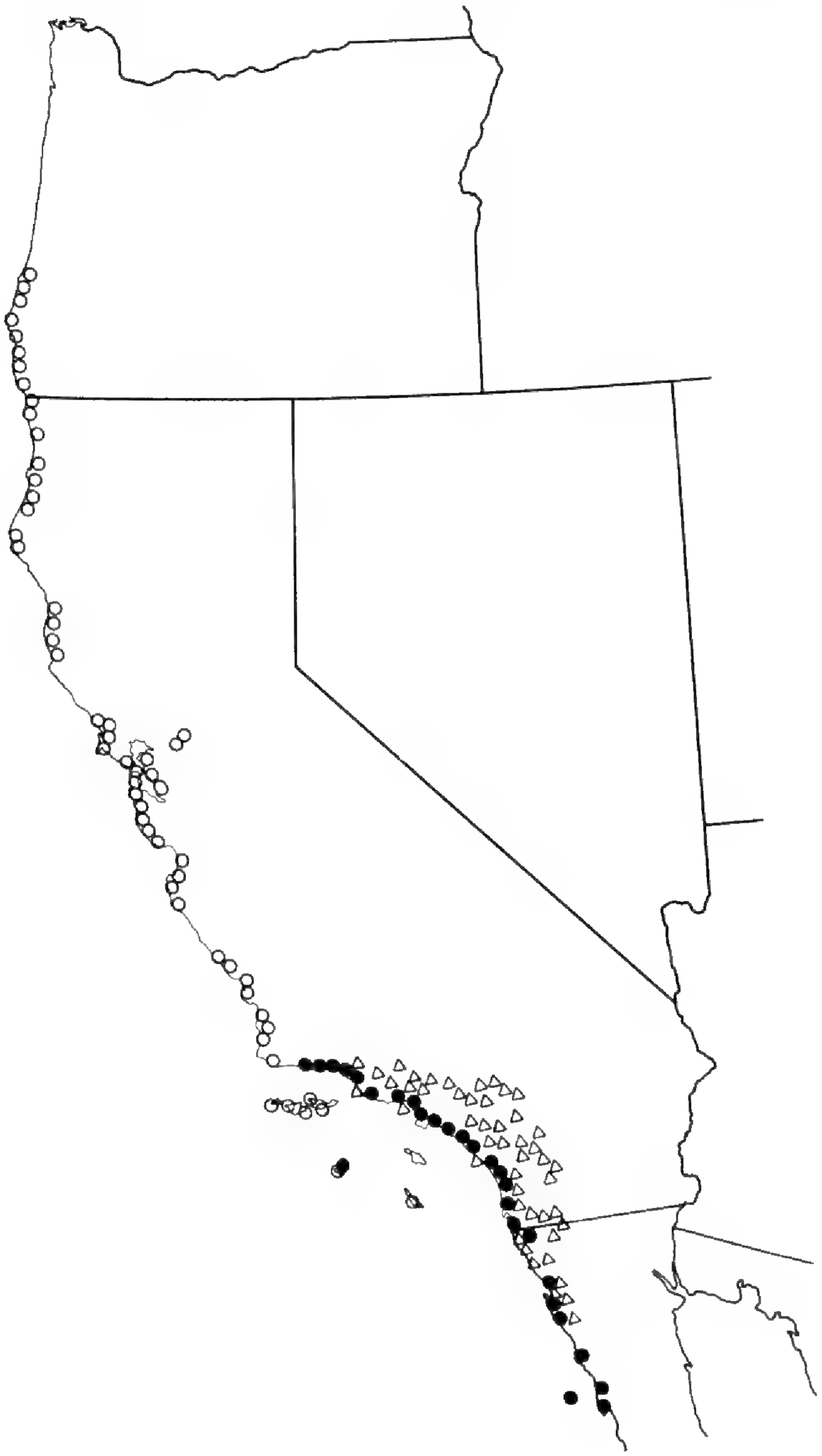


FIGURE 30.—Portion of the western United States and adjacent Mexico, showing the ranges of species of *Camissonia* sect. *Holostigma:* ●=*C. cheiranthifolia* subsp. *suffruticosa;* ○=*C. cheiranthifolia* subsp. *cheiranthifolia;* △=*C. bistorta.*

suffruticosa gave rise on the one hand to the self-incompatible, annual *C. bistorta* and on the other to the autogamous, perennial *C. cheiranthifolia* subsp. *cheiranthifolia.* An account of the anatomy of subsp. *suffruticosa* has been given by Purer, Ecol. Monogr. 6: 1–88. 1936.

At the present time, it occurs sympatrically with both of its presumed derivatives, and its relationship with subsp. *cheiranthifolia* has

been considered above. It also occurs sympatrically with *C. lewisii* at many localities.

Often *Camissonia bistorta* and *C. cheiranthifolia* subsp. *suffruticosa* occupy adjacent but sharply distinct habitats. At Point Dume, Los Angeles County, California, the former occurs on the upper reaches of the sandy beach and the latter forms colonies in the sandy grassland on the tops of the bluffs. Here the two do not grow immediately adjacent to one another, and intermediates have not been observed. On the other hand, where the habitats of the two species do intergrade more subtly, hybrids occur rather commonly. Populations of perennial plants otherwise resembling *C. bistorta* are characteristic of some areas and occur frequently along the entire coast of San Diego County, California, and in northern Baja California. Extensive series of intermediate populations occupy the sandy riverbeds in the vicinity of San Diego, a habitat that is clearly intermediate between the coastal dunes and flats inhabited by *C. cheiranthifolia* and the firmer sandy soil farther inland where *C. bistorta* occurs. Where intermediate plants do occur, they generally appear as relatively uniform local populations. The fertility of such plants is usually not reduced; for the collections indicated with an asterisk in the following list, pollen stainability was at least 96 percent for the average of two samples each of 200 pollen grains in cotton blue in lactophenol. In the Jones collection from Pacific Beach, pollen stainability was reduced to 79 percent; this collection might represent an F_1, or might be sterile for some other reason.

Specimens of apparent hybrids between *Camissonia cheiranthifolia* subsp. *suffruticosa* and *C. bistorta* examined:

U.S.: CALIFORNIA: SAN DIEGO CO.: Encinitas, *Lewis* 1202* (LA), *Epling & Robison* in 1932 (LA); Cardiff, *Benson* 10352* (POM); Oneonta, *Chandler* 5094 p.p. (NY); U.S. Hwy. 101 N. of La Jolla, *Benson* 4286 (POM); Valley Center, *Woodcock* in 1928 (SD); Crown Point near Pacific Beach, *Purer* in 1935 (POM)r Sunnyside, *Hall* 3908 (F); Foster, 400 ft., *Smith* 5257 (F); San Diego River nea; the Mission, *Abrams* 3412 (CAS, GH, LE, NMC, NY, PH, POM, UC); Mission Valley, *Purer* 6124 (DS, POM, SD), *Gander* 4929 (SD); Cuyamaca Road 0.5 mi. N. of Mission Gorge Road, San Diego R., Santee, *Wedberg* 533* (DS) El; Monte Park Grove, *Alderson* in 1934 (SD); San Luis Rey, *Gander* 3309 (;SD) foot of San Miguel Mt., *Youngberg* 44 (POM), *Gander* 154.5 (SD); S. San Diego, *Chandler* 5097 (DS, NY); wash between National City and Chula Vista, *Wolf* 2086 (DS, RSA, UC), *Gander* 4920 (SD); Otay Creek, 2 mi. below dam, *Peirson* 3410 (RSA); Otay, *Higgins* in 1954 (UC); Nestor, near Tia Juana, *Wiggins* 3229 (DS LA, UC).

BAJA CALIFORNIA: Dry Tijuana R. bed, 80 ft., *Smith* 5206 (F, PH); 2 mi. N. of Rosarito Beach, *Wiggins & Gillespie* 3882 (CAS, DS, F, GH, NY, POM, RSA); Descanso Dunes, R17059* (DS) *Higgins* in 1949 (RSA), in 1950 (RSA, SD), *Creighton* 525 (COLO), *Purer* in 1932 (SD); sea bluffs 32 mi. N. of Ensenada, *Munz* 22702 (RSA); Pinita, *Harbison* in 1950 (SD); Hot Springs, *Jones* in 1882 (POM, RM, UC); Cariso Creek, *T. S. Brandegee* in 1893 (UC).

These two entities have been hybridized experimentally, using a strain of *C. bistorta* from 6.5 miles east of San Juan Capistrano, Orange County, California (R18782), and one of *C. cheiranthifolia* subsp. *suffruticosa* from De Anza Cove, Mission Bay, San Diego County, California, collected by H. L. Wedberg. Both parental strains were self-incompatible, and both regularly formed 7 pairs of chromosomes at meiotic metaphase I. Seeds were readily obtained in both directions, but only those derived from the cross using *C. cheiranthifolia* as the female parent germinated. Four individuals from a large F_1 progeny were examined cytologically. The maximum association of chromosomes observed was a ring of 8 and 3 ring bivalents, with the large ring most often present as a chain and one of the bivalents being a rod (i.e., forming only one chiasma) in most cells. Samples of 200 pollen grains from each of three individuals, stained in cotton blue in lactophenol, gave the following percentages of apparently viable pollen: 24.5, 24.5, and 34.7%. Although the hybrids were self-incompatible like both of their parents, cross-pollination gave essentially full seed-set, and doubtless these plants would easily backcross with either parent, thus producing individuals similar to many of the putative hybrids observed in the field.

Two of the apparent hybrids (possibly backcrosses with *C. cheiranthifolia*) found in the field were examined cytologically and showed no evidence of structural heterozygosity:

BAJA CALIFORNIA: Meadows E. of Rosarito, *Bates* 2331; ca. 29 mi. S. of Tijuana, *Klein & Gregory* 1274* (RSA).

One of the early binomials applied to plants of this section was *Holostigma bottae* Spach, Nouv. Ann. Mus. Paris 4: 336. 1835. Its description is such that Munz (N. Amer. Fl. II. 5: 163. 1965) appropriately stated, "Possibly an earlier name for *Oenothera bistorta*" [= *Camissonia bistorta*]. Thus it is of considerable interest and importance to establish the identity of Spach's plant, with its type locality "In Californiâ australi." Through the kindness of Dr. Alicia Lourteig, I have been able to ascertain that there is apparently no specimen in the Paris herbarium annotated "*Holostigma bottae*." There is, however, a specimen collected by Paolo Emilio Botta at San Diego, California, in 1827, labeled (probably in Spach's hand) "*Sphaerostigma*." Spach used the names *Sphaerostigma* and *Holostigma* essentially interchangeably, and this appears to be the only specimen of the group present at Paris that was collected by Botta. Furthermore, it agrees perfectly and in detail with Spach's rather extensive description of *Holostigma bottae*. Consequently, I designate it the lectotype of this species.

Unquestionably, the specimen is one of the series of populations intermediate between *Camissonia bistorta* and *C. cheiranthifolia* subsp.

suffruticosa so common in the vicinity of San Diego and perfectly matched by many individuals growing today along the sandy bed of the San Diego River (e.g., *Wedberg* 533 or *Abrams* 3412, cited above). Its percentage of stainable pollen based on a sample of 200 grains, is 93%. In view of this, the name *Holostigma bottae* cannot be regarded as belonging to either of its parental species, and there seems no need to transfer it to *Camissonia* to serve as a binomial designation for the series of interspecific hybrids from which its type collection was derived more than 140 years ago.

26b. Camissonia cheiranthifolia subsp. **cheiranthifolia** FIGURES 28, 29

Oenothera cheiranthifolia Hornem. ex Spreng., Syst. 2: 228. 1825.

Oenothera spiralis Hook., Fl. Bor. Amer. 1: 213. 1833. Type: Coastal California (either at Trinidad Head, San Francisco, Santa Cruz, or Monterey), 1792–1794, *A. Menzies* (K).

Holostigma cheiranthifolium (Hornem. ex Spreng.) Spach, Nouv. Ann. Mus. Paris III. 4: 335. 1835.

Sphaerostigma cheiranthifolium (Hornem. ex Spreng.) Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 50. 1835.

Sphaerostigma spirale (Hook.) Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 50. 1835.

Agassizia cheiranthifolia (Hornem.) Spach, Hist. Nat. Vég. 4: 348. 1835.

Holostigma spirale (Hook.) Spach, Nouv. Ann. Mus. Paris III. 4: 336. 1835.

Oenothera nitida Greene, Pittonia 1: 70. 1887. Type: San Miguel I., Santa Barbara Co., Calif., September 1886, *E. L. Greene* (ND; isotypes, NY, PH, UC, US).

Sphaerostigma nitidum (Greene) Small, Bull. Torrey Cl. 23: 190. 1896.

Oenothera spiralis var. *nitida* (Greene) Jeps., Man. Fl. Pl. Calif. 684. 1925.

Oenothera cheiranthifolia var. *typica* Munz, Bot. Gaz. 85: 268. 1928.

Oenothera cheiranthifolia var. *nitida* (Greene) Munz, Bot. Gaz. 85: 269. 1928.

Branches usually prostrate or decumbent and largely herbaceous; pubescence rarely dense and silvery. Hypanthium 2.1–4.2 (–4.8) mm. long, 1.5–3 mm. across at the summit. Sepals 4–5.6 (–6.7) mm. long, 1.3–1.9 (–2.1) mm. wide. Petals 6–11 mm. long, 5–12 mm. wide, rarely with one or two red dots near the base. Filaments of the episepalous stamens 2.8–4.5 mm. long, those of the epipetalous ones 1.5–3 mm. long. Anthers 1–1.5 mm. long. Style 6–9 mm. long; stigma surrounded by both sets of anthers which shed pollen directly onto it at anthesis, or very rarely held above the anthers. Gametic chromosome number, $n=7$. Facultatively autogamous, but sometimes outcrossing; self-compatible.

LECTOTYPE: "Ex hort. semina e California mis. Wormskiold" (C), doubtless from seed collected in the vicinity of Fort Ross, Sonoma County, or San Francisco, California. During most of the 19th century, the species was erroneously attributed to Chile, based on Sprengel's statement in the protologue; no evidence for this has ever been found, and it is assumed that Sprengel made a simple mistake (cf. Munz, Bot. Gaz. 85: 268. 1928).

DISTRIBUTION (Figure 30): Sandy slopes and flats along the coast, from Coos Bay, Curry County, Oregon, south to Point Conception, Santa Barbara County, California; also on the east shore of San Francisco Bay in Alameda and Contra Costa Counties, California; sand dunes and flats along the lower Sacramento River, California, often with *Lupinus arboreus*, another beach species (4 miles west of Antioch, Contra Costa County, *Heller* in 1942, WTU; between Antioch and Rio Vista bridges, Sacramento County, *Eastwood & Howell* 8636, CAS; Brannan Island State Park, Sacramento County, R20178, DS); San Miguel, Santa Rosa, Santa Cruz, San Nicolas, and San Clemente Islands.

The gametic chromosome number of this subspecies has been determined as $n=7$, with no evidence of structural heterozygosity, in single individuals from eight populations throughout its range (see Appendix). Although self-pollination generally occurs in this taxon upon the closing of the flowers, some populations, especially in the San Francisco Bay area, are much visited by oligolectic bees of the genus *Andrena* (*Onagrandrena*) and are doubtless outcrossed to a large extent. Other populations, such as those around Monterey Bay and farther south, appear not to be visited often by insects of any kind and are probably predominantly self-pollinated. The flowers of subsp. *cheiranthifolia* generally open more tardily than those of subsp. *suffruticosa*, which also occupies areas where the mornings are not often foggy.

This subspecies is quite variable in pubescence, and there appears to be a cline extending from the San Francisco area, where the plants are usually decumbent and greenish, to the region of Morro Bay, San Luis Obispo County, where many of the plants are more erect and silvery pubescent, resembling indiviuals of subsp. *suffruticosa*. Such plants may also have larger flowers than usual for subsp. *cheiranthifolia* but in general are not exceptional in flower size.

Other variants in pubescence may occur as individual plants, mixed in populations of more usual individuals. For example, at the mouth of Hazard Canyon, San Luis Obispo County, California, Robert Hoover collected an interesting local race with large bright green but still pubescent leaves, up to 4.5 cm. long and 2 cm. wide, growing with the usual more heavily pubescent and smaller leaved plants. Occasional completely glabrous or subglabrous plants occur in populations; these individuals have been named *Oenothera nitida* Greene. Such plants agree with the rest of the species in chromosome number. They obviously comprise only one of the more conspicuous segregating elements in their interbreeding populations, and do not merit formal taxonomic recognition. Such glabrous plants have been collected around Monterey Bay, Monterey County, California, where

they are well known; in Santa Barbara County, California, at Surf (*Pierson* 8308, POM, RSA) and at Jalama Beach (*Smith* 2848, RSA); and on Santa Rosa (East Point, *Munz & Hoffmann* 11744, POM) and San Miguel Islands.

On San Martín Island, off the coast of Baja California, individuals of subsp. *suffruticosa* occur which are more prostrate than usual for that subspecies and thus resemble subsp. *cheiranthifolia: Moran* 10571 (ARIZ, COLO, BS, RSA, SD, UC). As these plants agree with other Baja California populations of subsp. *suffruticosa* in flower size and pubescence, I have regarded them as representing a maritime ecotype of that taxon. The possibility that they may in fact belong with subsp. *cheiranthifolia* and represent a relictual station for that more northern subspecies cannot, however, be completely ruled out at present. It does seem more likely that they have converged with it in habit on the basis of their similar ecology.

Camissonia cheiranthifolia subsp. *cheiranthifolia* occurs sympatrically with *C. micrantha*, and with *C. guadalupensis* subsp. *clementina* and locally intergrades with *C. cheiranthifolia* subsp. *suffruticosa* as discussed above.

27. Camissonia bistorta (Nutt. ex Torr. & Gray) Raven, Brittonia 16: 284. 1964. FIGURE 31

Oenothera heterophylla Nutt. ex Hook. & Arn., Bot. Beechey Voy. 341. 1938; non Spach 1835. Type: San Diego, San Diego Co., California, April-May 1836, *T. Nuttall* (BM).

Oenothera bistorta Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 508. 1840.

Sphaerostigma bistortum (Nutt.) Walp., Rep. 2: 77. 1843.

Oenothera bistorta var. *veitchiana* Hook., Bot. Mag. 84: *pl. 5078.* 1858. Lectotype: Plains about San Gabriel Mission, Los Angeles Co., California *W. Lobb* 416, grown at *Hort. Veitch* in 1857 (K).

Sphaerostigma veitchianum (Hook.) Small, Bull. Torrey Cl. 23: 191. 1896.

Sphaerostigma bistortum var. *veitchianum* (Hook.) A. Nels., Bot. Gaz. 40: 59. 1905.

Oenothera cheiranthifolia f. *delicatula* H. Lév., Monogr. Onoth. 216, fig. on p. 214. 1905.

Oenothera bistorta var. *typica* Munz, Bot. Gaz. 85: 266. 1928.

Annual, or rarely a short-lived perennial, with one to several ascending or several spreading, decumbent stems radiating from a central rosette, these to 0.8 mm. long, with a conspicuously exfoliating pale rhytidome. Plants strigose or more commonly villous. Leaves very narrowly elliptic in the basal rosette to narrowly lanceolate or lanceolate on the stems and in the inflorescence, rarely all linear, 1.2–12 cm. long, 0.15–1.5 cm. wide, denticulate, but often only sparsely and inconspicuously so, the apex acute, the base narrowly cuneate (in the basal rosette) to cuneate or subcordate; petioles to 4 cm. long in the basal rosette, the upper leaves usually subsessile. Inflorescence with two types of trichomes, short-erect and long-villous. Hypanthium

FIGURES 31–32.—Species of *Camissonia* sect. *Holostigma*, × 1: 31, *C. bistorta* (*Raven* 16935 DS); 32, *C. lewisii* (*Raven* 17021, DS).

2–5 (–7.5) mm. long, 1.5–4 mm. across at the summit, glabrous to pubescent in lower portions within, often with prominent red dots near the summit within. Sepals (2.3–) 5–8 (–11) mm. long, (0.8–) 1–2 mm. wide, reflexed in pairs. Petals (4.2–) 7–15 mm. long, (2.5–) 6.5–12 (–16) mm. wide, each petal almost always with a bright red spot (rarely two) near the base. Filaments of the episepalous stamens (1–) 1.5–3.5 mm. long, those of the epipetalous ones (0.5–) 1–2.5 mm. long; anthers (0.5–) 1.3–2 (–2.5) mm. long. Style (5.5–) 7–12 mm. long, usually glabrous but occasionally pubescent near the base; stigma (0.7–) 1–1.8 mm. in diameter, held well above the anthers at anthesis. Capsule 1.2–4 cm. long, 1.5–2.5 mm. thick, more or less quadrangular in transection, straight or somewhat contorted. Seeds 0.9–1 mm. long, 0.3–0.55 mm. thick. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: San Diego, San Diego County, California, April-May 1836, *T. Nuttall* (NY; isotypes, BM, K, GH, PH).

DISTRIBUTION (Figure 30): Sandy fields near the coast or clayey grassland, often in openings of coastal sage, from Piru Creek and the Ojai Valley in Ventura County south and east through southern Los Angeles, southwestern San Bernardino, Orange, western Riverside, and the western two-thirds of San Diego Counties, California, and south in cismontane Baja California to Ojos Negros and San Vicente, never far from the coast; reaching the margins of the desert in San Bernardino (near Hesperia) and San Diego Counties. Usually at low elevations, sea level to 2,000 ft., but exceptionally as high as 8,000 ft. alt. in the mountains, where it occurs about the borders of meadows. Collected as a waif beyond its main area in the Goleta salt marsh, Santa Barbara County, California, "Introduced apparently with Stream gravel . . . ," 20 June 1959, *Pollard* (CAS) and on ballast heaps at Nanaimo, Vancouver Island, British Columbia, 13 July 1893, *Macoun* (NMC). *Camissonia bistorta* has occasionally been cultivated in Europe, at least in the 19th century.

The chromosome number has been determined from 29 individuals derived from 22 populations scattered throughout the range of the species (see Appendix). Populations from 6.5 miles northeast of San Juan Capistrano, Orange County, California, R18782 (8 individuals); lower edge of Cleveland National Forest, just above San Juan Campground, Santa Ana Mountains, Orange County, California, R18783 (6 individuals); Point Dume, Los Angeles County (2 individuals); and Claremont, Los Angeles County, California (10 individuals), were grown in the experimental garden and found to be self-incompatible. In addition, the Claremont strain was grown by Hagen (Indiana Univ. Publ. Sci. Ser. 16: 309. 1950) who also found it to be self-incompatible. Several species of large bees of the genus *Andrena* sub-

genera *Diandrena* and *Onagrandrena* are frequent oligolectic visitors to the flowers of *Camissonia bistorta* soon after they open in the early morning and doubtless are the most important agents in effecting cross-pollination in this species.

Camissonia bistorta may well be an annual derivative of populations similar to the self-incompatible ones referred to *C. cheiranthifolia* subsp. *cheiranthifolia*, although the reverse hypothesis cannot be excluded at present. Depauperate individuals of this species, found in dry years or unfavorable sites, often have relatively small flowers, as do plants at the end of their flowering period. The stigma is, however, consistently held above the anthers, and such plants can thereby easily be separated from the numerous related autogamous species in sect. *Holostigma*. This species occurs sympatrically with *C. lewisii*, and a single obvious F_1 hybrid between the two species has been collected at Playa del Rey, Los Angeles County, California, *Wedberg* 272 (herb. San Diego State College). This plant had about 23 percent stainable pollen and apparently full seed-set; at meiosis it formed variable configurations of chromosomes, the maximum observed in 14 cells being 1 pair, 1 ring of 4, 1 chain of 3, and 5 univalents (H. L. Wedberg, pers. comm.). *Camissonia bistorta* also occurs adjacent to and hybridizes extensively with *C. cheiranthifolia* subsp. *suffruticosa*,

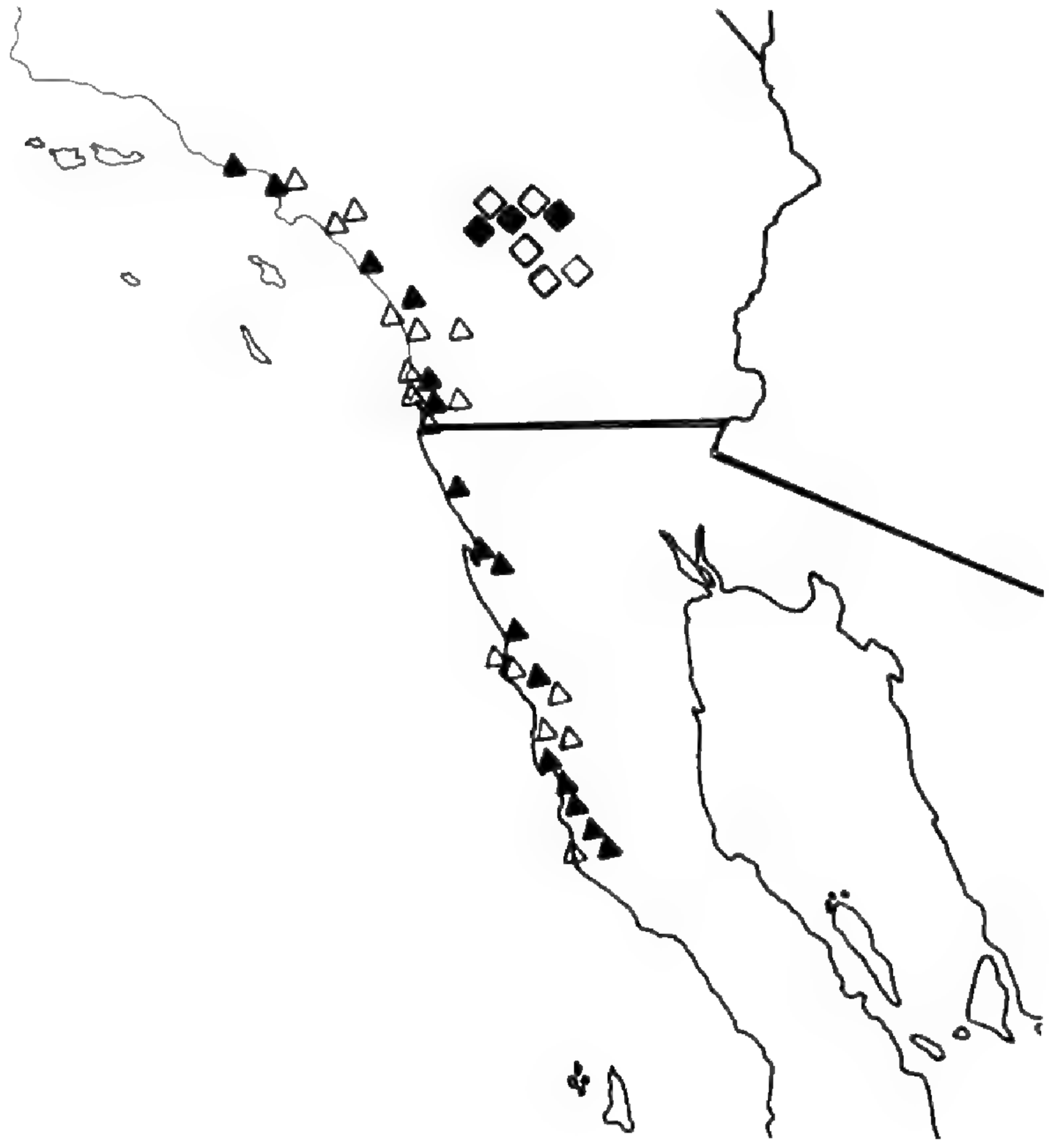


FIGURE 33.—California and Baja California, showing ranges of species of *Camissonia* sect. *Holostigma:* △=*C. lewisii*, with ▲=diploid chromosome counts ($n=7$); ◇=*C. pallida* subsp. *hallii* with ◆=diploid counts ($n=7$).

as explained in the section dealing with that taxon. It has likewise been observed growing sympatrically with *C. micrantha*, *C. hirtella*, *C. ignota*, *C. intermedia*, *C. confusa*, and *C. robusta*, but hybrids between these predominantly autogamous species and *C. bistorta* have not been found. *Camissonia bistorta* is probably relatively similar to the populations ancestral to at least some of the autogamous taxa in this section, the most obvious relationship being that with *C. lewisii*.

In his original treatment of this species (Bot. Gaz. 85: 266–267. 1928), Munz included two varieties in addition to the typical one. The first of these, *Oenothera bistorta* var. *veitchiana* Hook., was applied to inland populations with relatively slender, long, and straight capsules which differed in these respects from the series of coastal populations, including the type of the species, which have thicker, shorter, usually coiled capsules. These two entities intergrade so broadly that it does not appear useful to segregate them taxonomically. The other variety recognized by Munz, *O. bistorta* var. *hallii* (Davids.) Jeps., intergrades completely with the entity designated by Munz *O. hirta* var. *exfoliata* (A. Nels.) Munz and is here treated, together with that taxon, as the species *Camissonia pallida* (Abrams) Raven. *Camissonia pallida* and *C. bistorta* do not occur together, as far as I know, and, although both entities are diploid ($n=7$), there appears to be no evidence for morphological intergradation or even of overlapping patterns of variation.

The report of *Camissonia bistorta* from Santa Catalina Island, California (Millspaugh & Nuttall, Field Mus. Publ. Bot. 5: 183. 1923; as *Sphaerostigma bistortum*) is based on misidentified specimens of *C. robusta* and *C. californica*, which I have seen.

28. Camissonia guadalupensis (S. Wats.) Raven, Brittonia 16: 284. 1964.

Erect annual with short branches usually arising above the base; plants thick-stemmed, heavy-set, with conspicuously exfoliating epidermis, subsucculent, villous or strigose all over, 2–18 (–35) cm. tall. Leaves narrowly elliptic in the basal rosette to narrowly ovate on the stems and in the inflorescence, 1.2–3.8 (–9.5) cm. long, 0.5–1.2 (–1.8) cm. wide, sparsely and weakly denticulate, the apex acute (lower leaves) to obtuse (upper leaves), the base attenuate (lower leaves) to rounded or truncate (upper leaves); leaves subsessile. Inflorescence with short glandular trichomes in addition to the predominant sort found on other parts of the plant. Hypanthium 1.6–2.4 mm. long, 1.2–1.6 mm. across at the summit, sparsely pubescent with short erect trichomes in lower portions within. Sepals 1.9–3.2 mm. long, 0.8–1.6 mm. wide. Petals 2.8–4.2 mm. long, 2–3.6 mm. wide, sometimes with a prominent red dot near the base of each one. Filaments of the episepalous stamens 1.3–2.3 mm. long, those of the epipetalous ones 0.4–1.6 mm. long; anthers 0.4–0.8 mm. long. Style

3.2–4.5 mm. long, short-pubescent near the base; stigma 0.5–0.8 mm. in diameter, surrounded by the anthers at anthesis. Capsule 10–18 mm. long, 2.8–3.5 mm. thick near the base, very heavy in appearance, quadrangular in transection and deeply grooved along the lines of dehiscence, straight or slightly curved outward. Seeds 0.75–0.9 mm. long, 0.4–0.55 mm. thick. Gametic chromosome number, $n=7$. Autogamous.

DISTRIBUTION (Figure 36): Sandy flats, dunes, and arroyo bottoms, San Clemente Island, Los Angeles County, California (subsp. *clementina*), and Isla Guadalupe, Baja California (subsp. *guadalupensis*). Sea level to perhaps 1,200 ft. alt.

Reciprocal F_1 hybrids were made between progenies of R17628 (subsp. *clementina*) and *Moran & Ernst* 6737 (subsp. *guadalupensis*). These plants had a mixture of all three sorts of pubescence found in the two subspecies, the strigose pubescence of subsp. *guadalupensis*, however, being relatively sparse. The hybrids had a red dot near the base of each petal, as in subsp. *clementina*, but this was reduced in size. They appeared to have full seed-set, comparable to that of the parents. Two of the F_1 individuals in which subsp. *guadalupensis* was the pistillate parent (=R18771) and one in which subsp. *clementina* was the pistillate parent had 7 bivalents at meiotic metaphase I and diakinesis, and thus no evidence of chromosomal structural heterozygosity. The pollen stainability in cotton blue in lactophenol, calculated from a sample of 200 grains in each case, was measured in three plants in which subsp. *guadalupensis* was the pistillate parent and found to be 41.5, 49.5, and 41.5 percent; in two F_1 plants in which subsp. *clementina* was the pistillate parent, the percentages of stainable pollen were, respectively, 58 and 38 percent. As compared with the 98–100 percent stainable pollen found in samples taken from both parents grown under the same conditions, these figures indicate a substantial reduction in fertility in the hybrids, although seed-set does not appear to be impaired. Nonetheless, the very close morphological relationship between these two entities and their evident distinctiveness when compared with other species can seemingly best be indicated by retaining them within a single taxonomic species.

28a. Camissonia guadalupensis subsp. **guadalupensis** FIGURE 34

Oenothera guadalupensis S. Wats., Proc. Amer, Acad. 11: 115. 1876.

Oenothera guadalupensis subsp. *guadalupensis* Munz, N. Amer. Fl. II. 5: 160. 1965.

Pubescence strigose with some longer trichomes in inflorescence, but no glandular ones. Petals without red dot at base. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Isla Guadalupe, Baja California, February–May 1875, *E. Palmer* (GH).

FIGURES 34–35.—*Camissonia guadalupensis*, × 1: 34, *C. guadalupensis* subsp. *guadalupensis* (*Raven* 18175, DS); 35, *C. guadalupensis* subsp. *clementina* (*Raven* 17284, DS).

DISTRIBUTION (Figure 36): Isla Guadalupe, Baja California, known with certainty only from the sandy bed of Arroyo Melpomone, 900–1,300 ft. alt.

ADDITIONAL SPECIMENS EXAMINED:

BAJA CALIFORNIA: ISLA GUADALUPE: Bed of Arroyo Melpomone, *Moran* 12070 (SD), *Moran & Ernst* 6737 (SD); progeny of *Moran & Ernst* 6737, R17530 (DS), 18175 (DS).

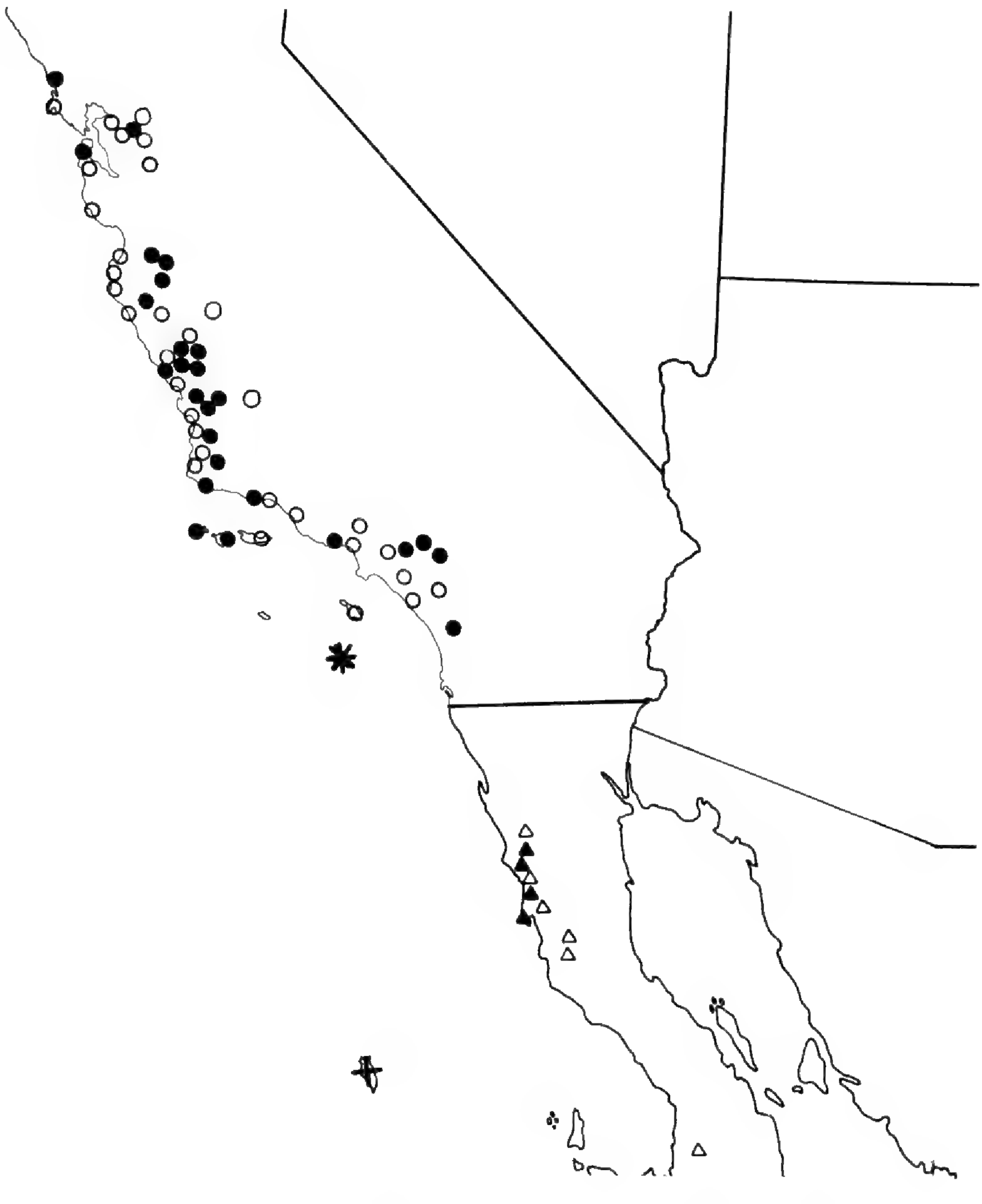


FIGURE 36.—Portion of the southwestern United States and northwestern Mexico, showing the ranges of species of *Camissonia* sect. *Holostigma;* +=*C. guadalupensis* subsp. *guadalupensis;* ✳=*C. guadalupensis* subsp. *clementina;* △=*C. proavita*, with ▲=diploid chromosome counts (*n*=7); ○=*C. micrantha*, with ●=diploid counts (*n*=7).

The chromosome number has been determined from two plants of this population, grown in the experimental garden (see Appendix). Plants of this subspecies were more highly autogamous than those of subsp. *clementina* when the two were grown in the experimental garden.

28B. Camissonia guadalupensis subsp. **clementina** (Raven) Raven, Brittonia 16: 284. 1964. FIGURE 35

Oenothera guadalupensis subsp. *clementina* Raven, Aliso 5: 332. 1963.

Pubescence dense, villous, with short glandular trichomes also present in the inflorescence. Petals each with a red dot near the base. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Common on pebbly dune above ocean south of Eel Point, San Clemente Island, elevation 40 ft., Los Angeles County, California, 9 April 1962, *P. H. Raven* 17125 (RSA).

DISTRIBUTION (Figure 36): Restricted to San Clemente Island, Los Angeles County, California, where it is common on dunes around the north end and down the west shore, perhaps to the south end; up to 100 ft. elevation.

ADDITIONAL SPECIMENS EXAMINED:

U.S.: CALIFORNIA: SAN CLEMENTE I., LOS ANGELES CO.: *Trask* 1684 (E, POM, US), *Murbarger* 154 (UC), *Piehl* 631101 (SBBG), *Blakley* 5224, 5254 (both SBBG), R17260, 17284, 17301, 17628, 17954, 18023 (all DS).

The chromosome number has been determined from single individuals of three populations, including the type collection (see Appendix). Plants of the subspecies were facultatively autogamous when grown in the experimental garden at Stanford, the flowers not selfing as early in the day on which they open as in subsp. *guadalupensis*. In the latter, the anthers scarcely left contact with the stigma at any time after opening. *Camissonia guadalupensis* subsp. *clementina* has been observed growing sympatrically with *C. cheiranthifolia* subsp. *cheiranthifolia*.

29. Camissonia lewisii Raven, sp. nov. FIGURE 32

Oenothera hirta var. *typica* Munz, Bot. Gaz. 85: 262. 1928; pro parte.

Oenothera micrantha sensu Munz, N. Amer. Fl. II. 5: 106. 1965; pro parte.

Herba annua villosa, ad *C. micrantha* similis, ramis plurimis decumbentibus e rosula centrali radiantibus, rariore caule singulari erecto; rami ad 0.6 m. longi. Folia 1–8 cm. longa. 0.2–1.1 cm. lata, denticulata. Inflorescentia pilis brevibus gladulosis longioribusque erectis patentibus pilosa. Hypanthium 1.5–4 mm. longum, ostio 1–2.5 mm. diameter. Sepala 1.7–3.5 mm. longa, 1–1.5 mm. lata. Petala (2.5 –) 3–5.5 mm. longa, (2–)2.5–5 mm. lata, plerumque prope basin puncto rubro uno vel duo. Filamenta staminum episepalorum 2–2.8 mm. longa, illa epipetalorum 1–1.7 mm. longa; antherae 0.7–1.2 mm. longae. Sylus 2.8–4.5(–5.5) mm. longus; stigma 0.7–1.8 mm. diametro, sub antheris circumnexum. Capsula 13–20 mm. longa, 1.8–2.2 mm. crassa, tran-

sectione valde quadrangularis in spiram laxam contorta. Semina 0.7–0.8 mm. longa, 0.5–0.6 mm. crasa, obovoidea. Chromosomatum numerus gameticus, $n=7$. Autogama.

TYPE: Common in open clayey grassland, with *Eschscholzia*, *Abronia*, and grasses, 1.1 mile north of Colonia Guerrero, elevation 200 ft., Baja California, 30 March 1962, *P. H. Raven* 17035 (DS; isotypes, RSA, US).

DISTRIBUTION (Figure 33): Open sandy and clayey grassland, coastal dunes and beaches, never far from the coast, from sea level to 1,000 ft. alt., Point Dume and the Los Angeles Basin, Los Angeles County, California, south to Cardón Grande at the northern edge of Territorio de la Baja California Sur.

SELECTED SPECIMENS EXAMINED:

U.S.: CALIFORNIA: LOS ANGELES CO.: Hollywood, *Davidson* 1437 (LAM); Inglewood, *Abrams* 3232 (DS, GH, LA, NMC, NY, PH, POM, UC, US); Roscoe, *Eastwood* 242 (CAS); Point Dume, *Mars* (LA); Ballona Harbor, *Abrams* 1192 (DS, POM); San Pedro, *Eastwood* 166 (CAS). ORANGE CO.: Santa Ana, *King* in 1908 (JEPS); Bee Canyon, Rancho Santa Ana, *Howell* in 1928 (RSA). SAN DIEGO CO.: Fallbrook, *Jones* in 1882 (DS, GH, NY, POM, RM, UC); Agua Hedionda, *Peirson* 3409 (DS, RM, RSA); 4.6 mi. E. of San Pasqual, R17406 (DS); El Segundo, *Purer* in 1931 (SD); San Luis Rey, *Gander* in 1937 (SD); Crown Point, *Gander* 143.8 (SD); Oneonta, *Chandler* 5094 p.p. (NY); Bird Rock, *F. E. & E. S. Clements* 184 (COLO, F, GH, NY, PH, UC, UCSB), 185 (COLO, F, GH, NY, PH, UC, UCSB); Point Loma, *Eastwood* in 1913 (CAS, GH, NY, US); Ocean Beach, *Brandegee* 1645 (CAS, F, GH, LE, NMC, NY, POM, RM, UC, US); 1.5 mi. from Jamul toward Otay Dam, *Wiggins* 1923 (DS).

BAJA CALIFORNIA: Tijuana valley, *Orcutt* 82 (F, GH, US); ranch 29 mi. SW. of Tijuana, *Jones* in 1925 (POM); Descanso Dunes, R17060 (DS); S. end of Ensenada Bay, R17006 (DS); 9.3 mi. S. of San Vicente, R17044 (DS); 2.5 mi. W. of San Vicente, *Kadish* in 1956 (LA); 7.4 mi. N. of Ejido México, R17041 (DS); 4 km. S. of Ejido México, R12230 (DS); 4 mi. W. of Colonia Guerrero, *Blakley* 6302 (DS, SBBG); Santo Domingo (Hamilton's Ranch and vicinity), *Wiggins* 4494 (CAS, DS, GH, LA, NY, POM, UC, US); near Red Rock above Hamilton's Ranch, *Thomas* 130 (DS, OSC); San Quintín, *Epling & Robison* in 1935 (DS, UC, NY), San Quintín Bay, 1889, *Palmer* 617 (CAS, F, GH, NY, PH, UC, US); Socorro, *Cronemiller* 3076 (DS, POM); 20.6 km. S. of road to San Quintín, R12396 (DS); 20 mi. N. of El Rosario, *Harbison* in 1935 (SD); 3.7 mi. E. of Punta Baja toward El Rosario, *Gregory* 356 (RSA); 16 km. SE. of El Rosario, R12466 (DS); El Cañón Rancho, near Calmallí, *Haines & Stewart* in 1935 (DS); El Poso Allemán, *Brandegee* in 1889 (UC); Cardón Grande, *Brandegee* in 1889 (UC).

Camissonia lewisii, an autogamous diploid species, can easily be recognized by its short, usually once-coiled capsules that are square in transection in living material. It is quite similar to some coastal populations of *C. bistorta*, such as those found in San Diego County, California, and may have been derived from populations of this sort. The chromosome number has been determined from 23 individuals representing 19 populations, scattered throughout the range of the

species, including the type collection (see Appendix). An apparent hybrid with *C. bistorta* was once collected, as discussed under that species, and *C. lewisii* likewise occurs sympatrically with *C. cheiranthifolia* subsp. *suffruticosa*, *C. proavita*, *C. micrantha* (at Point Dume and Playa del Rey, Los Angeles County, California), *C. ignota*, *C. intermedia*, and *C. robusta*. No hybrids with these species have been observed.

Camissonia lewisii is named in honor of Harlan Lewis, who introduced me to the study of Onagraceae when I was a graduate student at the University of California, Los Angeles. Judging from its morphology and distribution, this species is certainly one of the parents of the hexaploid *C. robusta*, which can, however, easily be distinguished by its more robust, erect habit, less sharply angled capsules, and high proportion of 4- and 5-pored pollen grains. *Camissonia lewisii* is probably not directly involved in the ancestry of any other polyploid species.

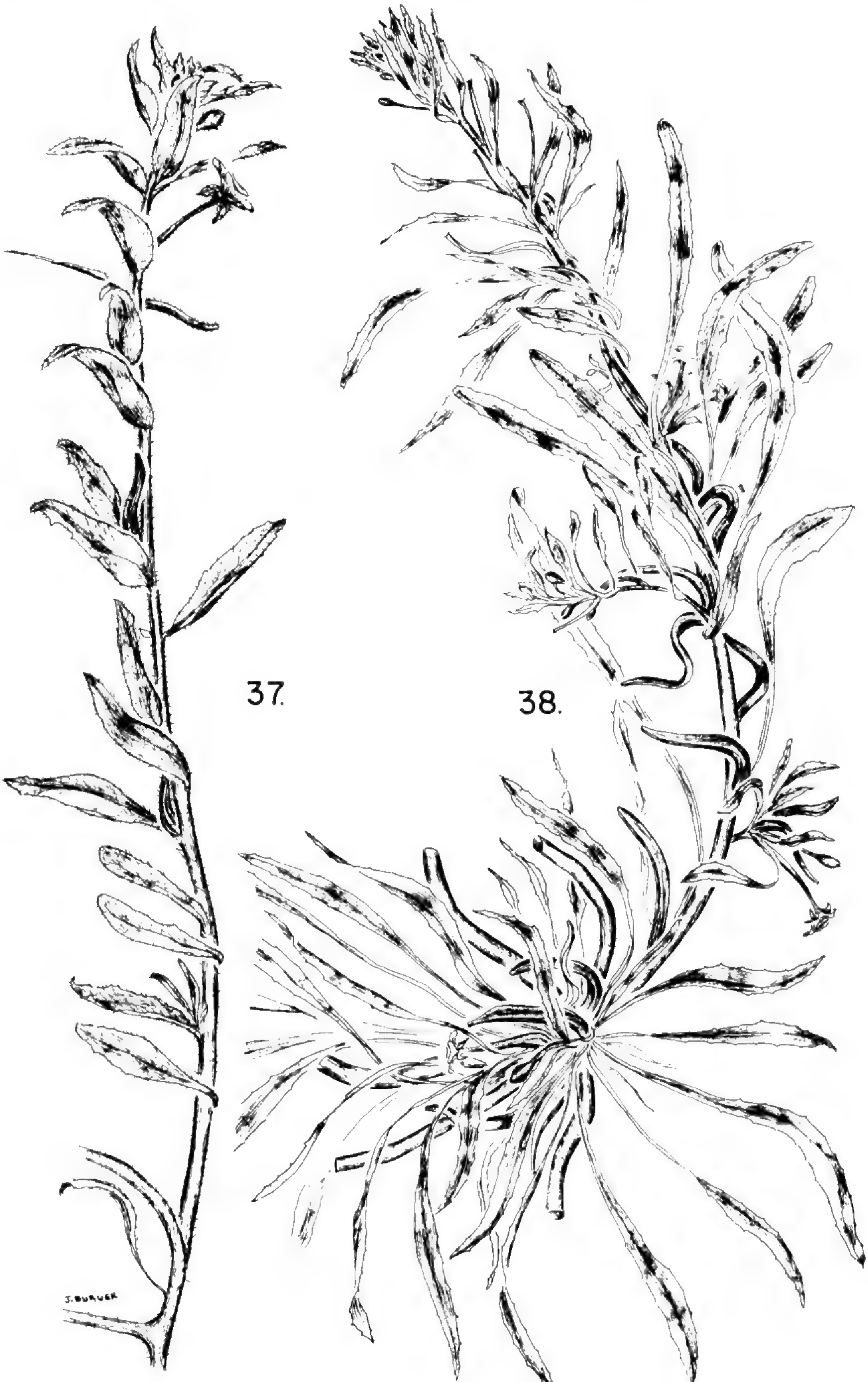
30. Camissonia proavita Raven, sp. nov. FIGURE 38

Oenothera hirta var. *typica* sensu Munz, Bot. Gaz. 85: 262. 1928; pro parte.
Oenothera micrantha sensu Munz, N. Amer. Fl. II. 5: 160. 1965; pro parte.

Herba annua sparsissime strigulosa, omnino eglandulosa, ad *C. micrantha* similis, rosula densissime florens, ramis prostratis crassiusculis ad 45 cm. longis tarde e rosula crescentibus. Folia conferta lineares vel angustissime elliptica, 2–9 cm. longa, 0.2–0.55 cm. lata, ad petiolum gradatissime attenuate, sparsissime denticulata; petiolus ad 2 cm. longus. Inflorescentia densiore strigulosa, conferta, interdum pilis paucis longioribus patentibus praedita. Hypanthium 1.2–1.8 mm. longum, ostio 1–1.2 mm. diametro. Sepala 1.8–2.8 mm. longa, 0.8–1.2 mm. lata. Petala 2.6–3.5 mm. longa, 1.8–2.2 mm. lata, immaculata. Filamenta staminum episepalorum 1.2–1.6 mm. longa, illa epipetalorum 0.5–1.3 mm. longa; antherae 0.6–0.8 mm. longae. Stylus 2–3.2 mm. longus; stigma 0.8–1 mm. diametro, sub anthesi antheris circumnexum. Capsula 15–20 mm. longa, 1.3–1.5 mm. crassa, transectione in sicco quadrangularis sed in vivo subquadrangularis, angulis subrotundatis; capsulae rosulae rectae, illae ramorum in spiram unam vel in spiras duas contortae. Semina 0.8–0.9 mm. longa, 0.5–0.6 mm. crassa. Chromosomatum numerus gameticus, $n=7$. Autogama.

TYPE: Disturbed soil by roadside, with *Orthocarpus purpurascens*, *Eschscholzia*, *Brassica*, near kilometer 201, 5.5 miles south of San Vicente, 950 ft., Baja California, 29 March 1962, *P. H. Raven* 17020 (DS; isotypes, RSA, US).

DISTRIBUTION (Figure 36): Sandy flats and dunes along the beaches or in the valleys up to 2,200 ft. alt., northern Baja California from the vicinity of San Vicente to near Misión San Borjas.



FIGURES 37–38.—Species of *Camissonia* sect. *Holostigma* × 1: 37, *C. micrantha* (*Raven* 18245, topotype, DS); *C. proavita* (*Raven* 17020, holotype, DS), showing only a portion of the dense central tuft and one of the branches.

ADDITIONAL SPECIMENS EXAMINED:

BAJA CALIFORNIA: 21 mi. S. of Santo Tomás, *Wiggins* 4273 (DS, NY, POM, US); San Telmo Plains, 7 mi. E. of San Telmo on road to Rancho San José (Meling's Ranch), *Wiggins* 9735A (DS); San Telmo, *Brandegee* in 1893 (UC); Los Alisos, ca. 5 mi. S. of Meling's Ranch, ca. 750 m, *Moran* 11341 (SD); San Quintín Bay, 1889, *Palmer* 656 (C, F, GH, NY, PH, US); 20.6 km. S. of road to San Quintín, R12397 (DS); near Rosario, *Orcutt* in 1886 (UC); 16 km. SE. of El Rosario, R12493; sandy wash at junction of El Mármol and San Fernando roads, 25 mi. W. of El Mármol, *Wiggins* 4343 (DS); Rancho Ramona, 29°53′N. lat., 115°06′W. long., *Huey* in 1958 (SD); San Borjas, *Brandegee* in 1889 (UC).

Camissonia proavita is an autogamous species obviously closely related to *C. micrantha* but easily distinguished by its very crowded habit and subglabrous vestiture. Most collected plants have no side branches and present a very dense cluster of 50 or more capsules in the basal rosette when mature. The branches are thicker than in any other member of the section, and the plant presents a very distinctive aspect at all stages of its life cycle. More than 200 miles separate the northernmost station of this species from the southernmost mainland locality of its close relative, *C. micrantha*.

The name "*proavita*" (=ancestor) was assigned to this species because of the hypothesis that it was one of the diploid ancestors of tetraploid populations of Baja California assigned in the present revision to *C. intermedia*, the other being *C. ignota*. At present, it appears more likely that all populations of *C. intermedia* have had a common allotetraploid origin involving *C. micrantha* and *C. hirtella*, but concrete evidence is not available to disprove the earlier hypothesis completely.

Camissonia proavita occurs sympatrically with *C. cheiranthifolia* subsp. *suffruticosa*, *C. lewisii*, *C. hirtella*, *C. ignota*, *C. intermedia*, and *C. robusta*, but no natural hybrids have been observed. The chromosome number of these species has been determined from 4 individuals, each from a different population, including the type collection (see Appendix).

31. Camissonia micrantha (Hornem. ex Spreng.) Raven, Brittonia 16: 284. 1964. FIGURE 37

Oenothera hirta Link, Enum. Hort. Berol. 1: 378. 1821; non *Oenothera hirta* L. 1760. Type: Seeds from California, grown in the Berlin Botanical Garden (authentic material, NY).

Oenothera micrantha Hornem. ex Spreng., Syst. 2: 228. 1825.

Holostigma micranthum (Hornem. ex Spreng.) Spach, Nouv. Ann. Mus. Paris 4: 335. 1835.

Sphaerostigma hirtum (Link) Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 22. 1835.

Sphaerostigma micranthum (Hornem. ex Spreng.) Walp., Rep. 2: 77. 1843.

Oenothera hirta var. *typica* Munz, Bot. Gaz. 85: 261. 1928.

Annual with sprawling branches up to 0.6 m. long from a basal rosette, or more rarely with a single erect stem. Plants more or less

densely villous all over. Leaves very narrowly elliptic in the basal rosette, the upper ones proportionately broader near the base but rarely broad enough to be called lanceolate, 1–12 cm. long, 0.2–1.7 mm. wide, denticulate, the apex acute, the base narrowly cuneate (in the basal rosette) to rounded; petioles of lower leaves to 2 cm. long, the upper leaves subsessile. Inflorescence more densely villous than the rest of the plant, usually grayish, rarely with an understory of short, glandular trichomes. Hypanthium 1.2–2 mm. long, 0.8–1.5 mm. across at the summit, a few trichomes within near the base. Sepals 1–2.2 (–2.5) mm. long, 0.4–1 mm. wide. Petals 1.5–3.5 (–4.5) mm. long, 0.8–2.2 (–2.5) mm. wide, occasionally with 1 or 2 red dots near the base. Filaments of the episepalous stamens 0.8–1.5 mm. long, those of the epipetalous ones 0.5–0.8 (–1) mm. long; anthers 0.4–0.6 mm. long. Style 2–3.5 mm. long, with a few trichomes near the base; stigma 0.5–0.6 mm. in diameter, surrounded by the anthers at anthesis. Capsule 1.3–2 (–2.5) cm. long, 1.1–1.2 (–1.8) mm. thick, subterete in living material but drying more or less quadrangular in transection, straight or curved in up to slightly more than one complete spiral. Seeds 0.7–1.1 mm. long, 0.3–0.6 mm. thick. Gametic chromosome number, $n=7$. Autogamous.

LECTOTYPE: Grown in the Copenhagen Botanical Garden, probably in 1821, from seeds doubtless collected in the vicinity of Fort Ross, Sonoma County, California (probably at Bodega Bay) (C).

DISTRIBUTION (Figure 36): Endemic to California, where it grows on coastal dunes and beaches or away from the ocean in sandy fields and in washes, from the vicinity of Bodega Bay, Sonoma County, and near Rio Vista, Sacramento County, south in the Coast Ranges to the Los Angeles Basin and the northern edge of San Diego County; also on San Miguel, Santa Rosa, Santa Cruz, and Santa Catalina Islands. From sea level to about 1,000 ft. alt. very rarely up to about 2,500 ft. Also collected once, probably on ballast heaps, in the vicinity of Nanaimo, Vancouver Island, British Columbia, 13 July 1893, *Macoun* (BM). Rather widely grown in European botanical gardens from the 1820s to the present, as a curiosity.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: CONTRA COSTA CO.: San Leandro, *Edwards* in 1877 (NY); Strawberry Canyon, Berkeley Hills, ca. 1,300 ft., R8982 (CAS); sand hills E. of Antioch, *Heller* 8892 (DS, F, GH, NY, PH, US, WTU); near Byron, *Heller* 14496 (DS). FRESNO CO.: Los Gatos Canyon 4 mi. N. of Coalinga, *Howell* 5804 (CAS). KERN CO.: Alec Cook Rocks, Cedar Canyon, 2,200 ft., *Twisselmann* 1194 (CAS). LOS ANGELES CO.: Big Tujunga wash, *Abrams* 1390 (DS, POM); Pomona, *Munz et al.* 2300 (DS, POM); Playa del Rey, *Ewan* 7536 (DS, LA, RM, UC); mouth of Hamilton Canyon, Santa Catalina I., *Fosberg* S4315 (F, LAM, NY, PH, POM, SBM, UC, US); Avalon, Santa Catalina I., *Trask* in 1898 (US). MARIN CO.: Near Radio Station, Pt. Reyes Peninsula, *Howell* 20956 (CAS, RSA). MON-

TEREY CO.: Near Del Monte, *Heller* 6659 (DS, F, GH, LE, NY, PH, POM, UC, US); San Ardo, *Hardham* 10004 (DS); Pajaro Hills, *Chandler* 386 (UC); 20 mi. from Carmel up Carmel R., road to Tassajara Springs, *Wolf* 3773 (UC); Pacific Valley, Santa Lucia Mts., *Plaskett* in 1898 (CAS); Vineyard Canyon Road 12 mi. W. of Parkfield, *Wiggins* 8020 (DS, GH, UC); Los Laurelos Road, 8 mi. N. of Carmel Valley, ca. 600 ft., *Rose* 57052 (COLO, RSA, US); Sycamore Canyon, 1 mi. S. of Big Sur State Park, *Bristol* 27 (Fresno State College herb.). ORANGE CO.: Bryant Ranch, *Wolf* 3778 (DS, RSA). RIVERSIDE CO.: Elsinore, *McC.* in 1892 (DS); 1.4 mi. W. of junction of Hwy. 60 with Van Buren Ave., *Wedberg* 227 (San Diego State College herb.). SACRAMENTO CO.: Brannan I. State Park, near Rio Vista, R20177 (DS). SAN BENITO CO.: About 4 mi. N. of Pinnacles Lodge, *Baker* 9282 (RSA). SAN BERNARDINO CO.: Red Hill near Upland, *Johnston* 1196 (DS, POM, UC, US). SAN DIEGO CO.: U.S. Hwy. 395, 2 mi. S. of turn to Lilac, R16950, R17457 (both DS). SAN FRANCISCO CO.: Fleishacker Pool, *Abrams* 12192 (DS; basis for *fig. 3434* in Abrams, Ill. Fl. Pac. States 3: 203. 1951). SAN JOAQUIN CO.: Corral Hollow, *Hoover* 3034 (UC). SAN LUIS OBISPO CO.: Baywood Park, Morro Bay, *Hardham* 9072 (DS, RSA); 3 mi. E. of Santa Margarita, *Linsley & MacSwain* 59–84 (RSA, UC); 10 mi. E. of Creston on La Panza Road, *Hoover* 7099 (RSA); Arroyo Grande, *Brewer* 446 (GH, UC, US). SAN MATEO CO.: San Pedro, *Elmer* 4813 (ARIZ, CAS, DS, NY, OSC, POM, UC, US); Ano Nuevo Point, *Thomas* 10178 (DS). SANTA BARBARA CO.: 5 mi. S. of Surf, *Ferris* 7543 (DS, POM, UC); 5 mi. from Lompoc, *Munz* 9269 (C, POM); Fox Canyon, Santa Barbara, *Smith* 1698 (RSA, WTU); 3 mi. S. of Carpinteria, *Lewis* 1298 (LA); San Miguel I., *Blakley* 5083 (DS, SBBG); Santa Rosa I., Water Canyon, *Munz & Crow* 11694 (GH, LA, OSC, POM, RSA); Santa Cruz I., vicinity of Pelican Bay, *Abrams & Wiggins* 41 (CAS, DS, GH, UC). SANTA CRUZ CO.: Ben Lomond sand hills, *Rose* 33241 (WTU); ca. 3.5 mi. W. of Watsonville, *Thomas* 3104 (DS, RSA). SONOMA CO.: Bodega Point, *Eastwood* 4831 (CAS, GH, PH). VENTURA CO.: Beach near mouth of Ventura R., *Pollard* in 1947 (COLO, RSA).

Camissonia micrantha is a diploid, autogamous species which has in the past been interpreted much more broadly (Munz, Bot. Gaz. 85: 260–265. 1928), including all species of this section except *C. cheiranthifolia*, *C. bistorta*, and *C. guadalupensis*. As interpreted here, it includes most of the material referred by Munz (loc. cit.) to *Oenothera hirta* var. *hirta*, excluding mostly collections of the tetraploid *C. intermedia*, which in part blurs the morphological distinctions between its two diploid ancestors, *C. micrantha* and *C. hirtella*. The chromosome number of *C. micrantha* has been determined in 47 individuals representing 39 populations from throughout the range of the species (see Appendix).

Camissonia micrantha is most closely related to the allopatric *C. proavita*, as discussed under that species. It is one of the diploid ancestors not only of the tetraploid *C. intermedia*, as just mentioned, but has probably combined with this tetraploid to give rise to the hexaploid *C. hardhamiae*. *Camissonia micrantha* occurs sympatrically with *C. cheiranthifolia* subsp. *cheiranthifolia*, *C. bistorta*, *C. lewisii*, *C. hirtella*, *C. intermedia*, *C. confusa*, *C. hardhamiae*, *C. luciae*, and *C. robusta*, but no hybrids with any of these species have been observed.

The populations of *C. micrantha* growing on the coastal dunes and beaches of northern Marin and southern Sonoma Counties consist of plants that are more robust and larger flowered than those found farther south. Such plants match the type material very closely and also are identical with plants grown from seed sent from the Copenhagen Botanical Garden and grown at Stanford (R18242). These seeds may have been derived from direct descendants of the original introductions, the species apparently having been in cultivation in Europe continuously since the 1820s.

32. Camissonia hirtella (Greene) Raven, Brittonia 16: 284. 1964.

FIGURES 39, 40

Oenothera hirtella Greene, Fl. Francisc. 215. 1891.

Sphaerostigma hirtellum (Greene) Small, Bull. Torrey Cl. 23: 190. 1896.

Sphaerostigma arenicola A. Nels. ("arenicolum"), Bot. Gaz. 40: 58. 1905. Type: Tassajara Hot Springs, Santa Lucia Mts., Monterey Co., Calif., June 1901, *A. D. E. Elmer* 3192 (DS: isotype, US).

Oenothera hirta var. *jonesii* H. Lév., Monogr. Onoth. 213. 1905. Lectotype: Drytown, Amador Co., Calif., 500 ft., *G. Hansen* 543 (DS; isotypes, NY, POM, UC. Cf. A. Nelson, Bot. Gaz. 40: 59. 1905).

Sphaerostigma micranthum var. *jonesii* (H. Lév.) A. Nels., Bot. Gaz. 40: 59. 1905.

Sphaerostigma bistortum var. *reedii* Parish, Muhlenbergia 3: 60. 1907. Lectotype: Waterman Road, 3,000 or 3,500 ft., San Bernardino Mts., San Bernardino Co., Calif., *S. B. Parish* 5794 (isotypes, GH, NY, UC).

Sphaerostigma hirtellum var. *montanum* Davidson, Muhlenbergia 3: 108. 1907.

Oenothera micrantha var. *hirtella* (Greene) Jeps., Man. Fl. Pl. Calif. 684. 1925.

Oenothera micrantha var. *reedii* (Parish) Jeps., Man. Fl. Pl. Calif. 684. 1925.

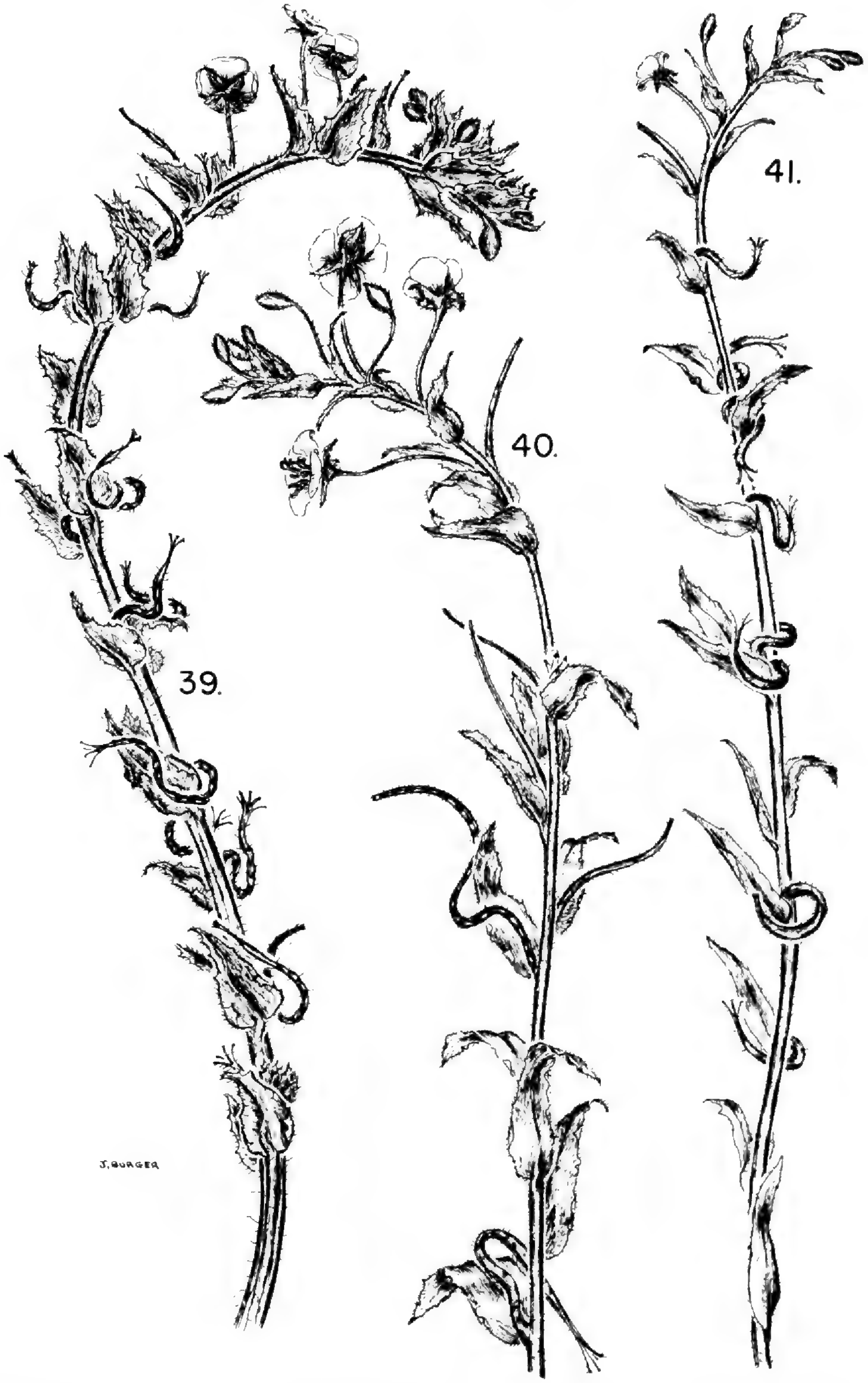
Oenothera hirta var. *jonesii* f. *reedii* (Parish) Munz, Bot. Gaz. 85: 263. 1928.

Oenothera micrantha var. *jonesii* (H. Lév.) Munz, Amer. Journ. Bot. 19: 778. 1932.

Erect annual, generally similar to *C. micrantha*, with one or more ascending branches from the basal rosette. Upper leaves narrowly ovate or ovate (rarely lanceolate), the apex acute, the base cordate to truncate. Inflorescence almost always with an understory of short glandular trichomes. Hypanthium 1–3 mm. long, 1–3 mm. across at the summit. Sepals 2.5–6 mm. long, 0.6–2 mm. wide. Petals 2–9 mm. long, 1.3–7 mm. wide, sometimes red-dotted near the base, occasionally with a salient tooth arising from the emarginate apex. Filaments of the episepalous stamens 1.2–6 mm. long, those of the epipetalous ones 0.5–3 mm. long; anthers 0.4–1 mm. long. Style 2–8 mm. long; stigma 0.5–1 mm. in diameter, surrounded by the anthers at anthesis. Capsule 0.75–0.9 mm. thick, terete, once or twice contorted. Gametic chromosome number, $n=7$. Autogamous, rarely cleistogamous.

LECTOTYPE: Mt. Hamilton, Santa Clara County, California, July 1891, *E. L. Greene* (ND).

DISTRIBUTION (Figure 42): On brushy hills and slopes, often locally abundant on burns, from Trinity and Amador Counties southward



FIGURES 39–41.—Species of *Camissonia* sect. *Holostigma*, × 1: 39–40, *C. hirtella:* 39, small flowered plant (*Raven* 17473, DS); 40, large-flowered plant (*Raven* 17416, DS). 41 *C. robusta* (*Raven* 17043, DS).

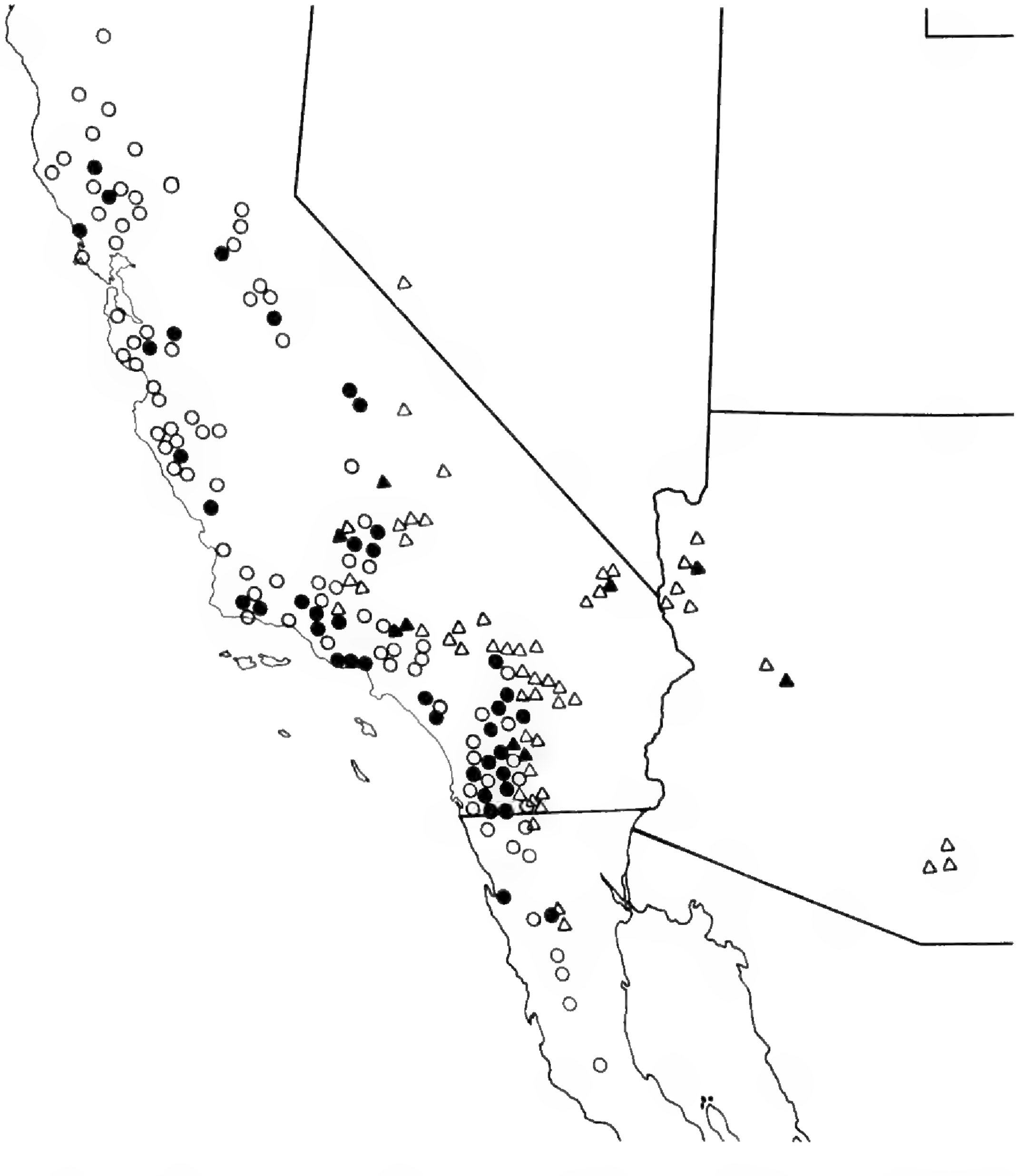


FIGURE 42.—Portion of the southwestern United States and northwestern Mexico, showing the ranges of species of *Camissonia* sect. *Holostigma*: ○=*C. hirtella*, with ●=diploid chromosome counts ($n=7$); △=*C. pallida* subsp. *pallida*, with ▲=diploid counts ($n=7$).

in the Coast Ranges and Sierra Nevada of California to the Sierra Juárez and Sierra San Pedro Mártir (south to ca. 30°45′ N. lat.) of Baja California, as well as the hills to their west; usually away from the immediate coast and barely reaching the margins of the desert. From near sea level to 7,500 ft. alt.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: AMADOR CO.: 6 mi. N. of Jones Butte, 450 ft., *Roseberry* 121 (RSA, UC); Ione, *Hoover* 2416 (RSA, UC). CALAVERAS CO.: Cosumnes R., *Rattan* 6420; Mokelumne Hill, *Blaisdell* (CAS, GH, NY, US). ELDORADO CO.: Coloma, *Eastwood* 14168 (CAS). FRESNO CO.: Tehipite Valley, *Hall & Chandler* 508

(UC). GLENN CO.: Grade ca. 10 mi. E. of Alder Springs, *Heller* 11443 (CAS, DS, F, GH, NY, OSC, UC, WTU). KERN CO.: W. end of Teyuca Ridge, 6,800 ft. *Twisselmann* 9576 (DS); Breckenridge Mt., 7,400 ft., *Twisselmann* 4704 (CAS, LA); 1 mi. E. of Havilah, 3,600 ft., R17569 (DS); Erskine Creek, *Purpus* 5099 (GH, UC, US); 8–10 mi. E. of Caliente, *Thorne* 31714 (RSA); 5 mi. E. of Alta Sierra, ca. 5,000 ft., Greenhorn Mts., *Thorne* 31772 (RSA). LAKE CO.: W. base of Snow Mt., *Ackley* in 1965 (CAS); foot of Mt. Sanhedrin, *Reynolds* (CAS); Kelsey Creek, Kelseyville, *Benson* 2178 (POM); 2 mi. W. of Houghs Springs, *Abrams* 12483 (DS); Cobb Mt. to Adams Springs on the Binkley Ranch, *Jussel* 154 (CAS, POM, UC). LOS ANGELES CO.: Mandeville Canyon, Santa Monica Mts., *Anderson & Epling* in 1930 (F, LA, US); San Dimas Canyon, 1,500 ft. *Munz & Harwood* 3686 (POM, UC, WTUS); Soledad Canyon between Acton and Ravenna, *Craig* 480 (POM); Bear Canyon Trail to Mt. San Antonio, *Craig* 415 (POM, UC). MADERA CO.: State Hwy. 41, S. of junction with Bass Lake road, *Wedberg 441* (San Diego State College herb.). MARIN CO.: Mill Valley, *Bioletti* in 1892 (RM). MARIPOSA CO.: Mt. Bullion, 2,300 ft., *Jepson* 10722 (JEPS). MENDOCINO CO.: Anderson Valley, *Purdy* in 1882 (GH); summit on road between Ukiah and Boonville, 2,300 ft., *Swensen* 39 (UC). MONTEREY CO.: 3 mi. up Salinas R. from Monterey, *Peirson* 3793 (DS, RSA); Pajaro Hills, *Chandler* 436 (UC); Hanging Valley, Arroyo Seco Road, 3,000 ft., *Hardham* 10871 (DS, RSA); between Junipero Serra and Pinyon Peaks, 4,700 ft., *Howell* 30177 (CAS); Big Sur, *Baker* 7863 (CAS). NAPA CO.: Ridge W. of Oakville, ca. 500 ft., *Reed* 325 (UC, WTU); near Knoxville, *Jepson* in 1892 (UC); La Jota, Howell Mt., *Jepson* 17569 (JEPS). ORANGE CO.: Glen Ivy Trail to Santiago Peak, 4,000 ft., *Munz* 7064 (POM, UC). RIVERSIDE CO.: Junction Main Divide Truck Trail with Ortega Hwy., 2,300 ft., Santa Ana Mts., R17762 (DS); Chalk Hill, 5,000 ft., San Jacinto Mts., *Hall* 2089 (UC); W. of Lake Elsinore, 1,600 ft., *Munz* 5086 (POM). SAN BENITO CO.: Near Hernandez, *Dudley* in 1899 (DS); Chalone Creek, Pinnacles National Monument, *Burgess* 238 (UC); brushy slopes of San Benito Peak above New Idria Mine, 4,000 ft., *Lyon* 919 (UC). SAN BERNARDINO CO.: Devore, mouth of Cajon Canyon, 600 m, *Munz* 11054 (C, GH, POM, UC, US); near Big Bear L., 6,000 ft., *Goodman & Hitchcock* 1743 (NY); Fredalba, *Abrams* 2791 (DS, GH, LE, NMC, NY, PH, US). SAN DIEGO CO.: Above Henshaw Dam, Palomar Mts., 3,500 *Munz* 8334 (GH, NY, POM); Cuyamaca L., 4,700 ft., *Munz & Harwood* 7276 (POM); Laguna Junction, *Epling et al.* in 1932 (DS, LA, UC); 10 mi. W. of Campo, 3,000 ft., *Munz* 12633 (POM). SAN LUIS OBISPO CO.: 4.5 mi. NE. of Santa Margarita, R20158 (DS); Bryson, Santa Lucia Mts., *Hardham* 10728 (DS); Arroyo Grande, *Brewer* 443 (US); McChesney Peak, 3,500–4,000 ft., *Hardham* 11040 (DS). SANTA BARBARA CO.: Junction of Zaca Ridge and Catway roads, Figueroa Mt., San Rafael Mts., 4,200 ft., *Blakley* 4300 (CAS, RSA, SBEG); Carpinteria, *Jones* in 1929 (POM); S. slope of Santa Ynez Peak, Santa Ynez Mts., 3,700 ft., *Breedlove* 2696 (CAS); Cuyamaca Valley 55 mi. E. of Santa Maria, *Munz* 11417 (POM); Pelican Bay, Santa Cruz I., *Clokey* 5010 (DS, GH, NY, POM, SD, US). SANTA CLARA CO.: Sierra Azul Ridge near Loma Prieta, 3,600 ft., *Hichborn* in 1920 (DS); Rattan's Ranch, near San Jose, *Rattan* in 1885 (DS, RSA); Colorado Creek, Red Mts., 2,500 ft., Mt. Hamilton Range, *Sharsmith* 3800 (UC). SANTA CRUZ CO.: 1 mi. up Boulder Creek from town of Boulder Creek, *Thomas* 1780 (DS, OSC, RSA); Ben Lomond Mt., 2,500 ft., *Thomas* 3471 (DS, OSC, RSA). SOLANO CO.: Summit Vaca Mts. via Collins Camp, *Jepson* 14482 (JEPS). SONOMA CO.: Petrified Forest, *Eastwood* 4618 (CAS). SUTTER CO.: North Butte, Marysville Buttes, *Bacigalupi* 2241 (DS). TEHAMA CO.: W. of Paskenta along logging road, *Wagnon* 12659 (RSA). TRINITY CO.: The Knob, near Deer Lick Springs, *Kildale* in 1931 (DS). TULARE CO.: Road to Mineral King, ca. 5,000 ft., *Baker* 4195a

(DS). TUOLUMNE CO.: South Fork Bridge, Tuolumne R., *Grant* 843 (JEPS). VENTURA CO.: Upper Sespe Creek, N. of Wheelers Hot Springs, 3,500 ft., *Munz* 13189 (POM, UC); Goodenough Meadow, Mt. Pinos region, *Dudley & Lamb* 4698 (DS); between Nordhoff and Big Chief peaks, ca. 4,000 ft., *Pollard* in 1945 (CAS); burn near Kennedy Canyon, *Pollard* in 1946 (ARIZ, CAS, SBM).

BAJA CALIFORNIA. 13 mi. SE. of Tecate, *Munz* 9516 (POM); 50 mi. SE. of Tecate, *Munz* 9558 (POM, US); 9 mi. W. of La Rumorosa, 4,020 ft., *Hevly & Pitman* 2053 (ARIZ); 3.5 mi. E. of Rancho San José (Meling's Ranch), *Wiggins* 9787 (DS, UC, US); 19.5 km. SE. of San Vicente, 400 m, R12285 (DS); 10 mi. N. of La Huerta, pine-oak belt, 4,000 ft., *Wiggins* 11845 (DS, OSC, SD, UC); 1 mi. NE. of Santa Catarina, 64 mi. SE. of Ensenada, ca. 3,875 ft., *Broder* 683a (DS, UCSB); Los Emes, S. Sierra San Pedro Mártir, 3,500 ft., *Wiggins* 9903 (DS, UC, US).

As I conceive it, this taxon includes most of the populations generally referred to *Oenothera micrantha* var. *jonesii* (H. Lév.) Munz. As discussed under *Camissonia micrantha*, the tetraploid *C. intermedia* in part bridges the morphological hiatus between its two putative diploid parents, *C. micrantha* and *C. hirtella*, and thus renders the separation of all three taxa difficult. The chromosome number of *Camissonia hirtella* was determined in 84 individuals derived from 76 populations scattered throughout the range of this species (see Appendix).

This widely distributed species is extremely variable in flower size, some individuals having petals up to 9 mm. long. Even in a collection with such large flowers, like R19076 (grown from R17402) from San Diego County, California, the longer set of anthers surrounds the stigma and deposits pollen directly on it, and the plants are fully self-compatible, setting a full complement of seed even when protected from insects. Insects are in general very rare at the flowers of this species.

In addition to being one of the diploid parents of the tetraploid *C. intermedia*, *Camissonia hirtella* has very probably combined with the diploid *C. pallida* subsp. *pallida* to give rise to the tetraploid *C. confusa*, and with one of these two tetraploids to give rise to the hexaploid *C. luciae*. *Camissonia hirtella* occurs sympatrically with *C. bistorta*, *C. micrantha*, *C. ignota*, *C. pallida* subsp. *pallida*, *C. intermedia*, *C. confusa*, *C. hardhamiae*, *C. luciae*, and *C. robusta*.

At times it is difficult to distinguish relatively narrow-leaved strains of this species from *C. intermedia*. For example, some populations from the central Sierra Nevada foothills of Calaveras County, California (e.g., *Quick* 52–01, CAS, 0.5 mile from Parrots Ferry bridge on road to Vallecito), temporarily referred here, might actually prove to be *C. intermedia* if their chromosome number could be determined. Similarly, *Heller* 7337 (DS, F, GH, LE, NY, OSC, PH, RM, UC, US), a widely distributed gathering from the foothills west of Los Gatos, Santa Clara County, California, might belong to either species.

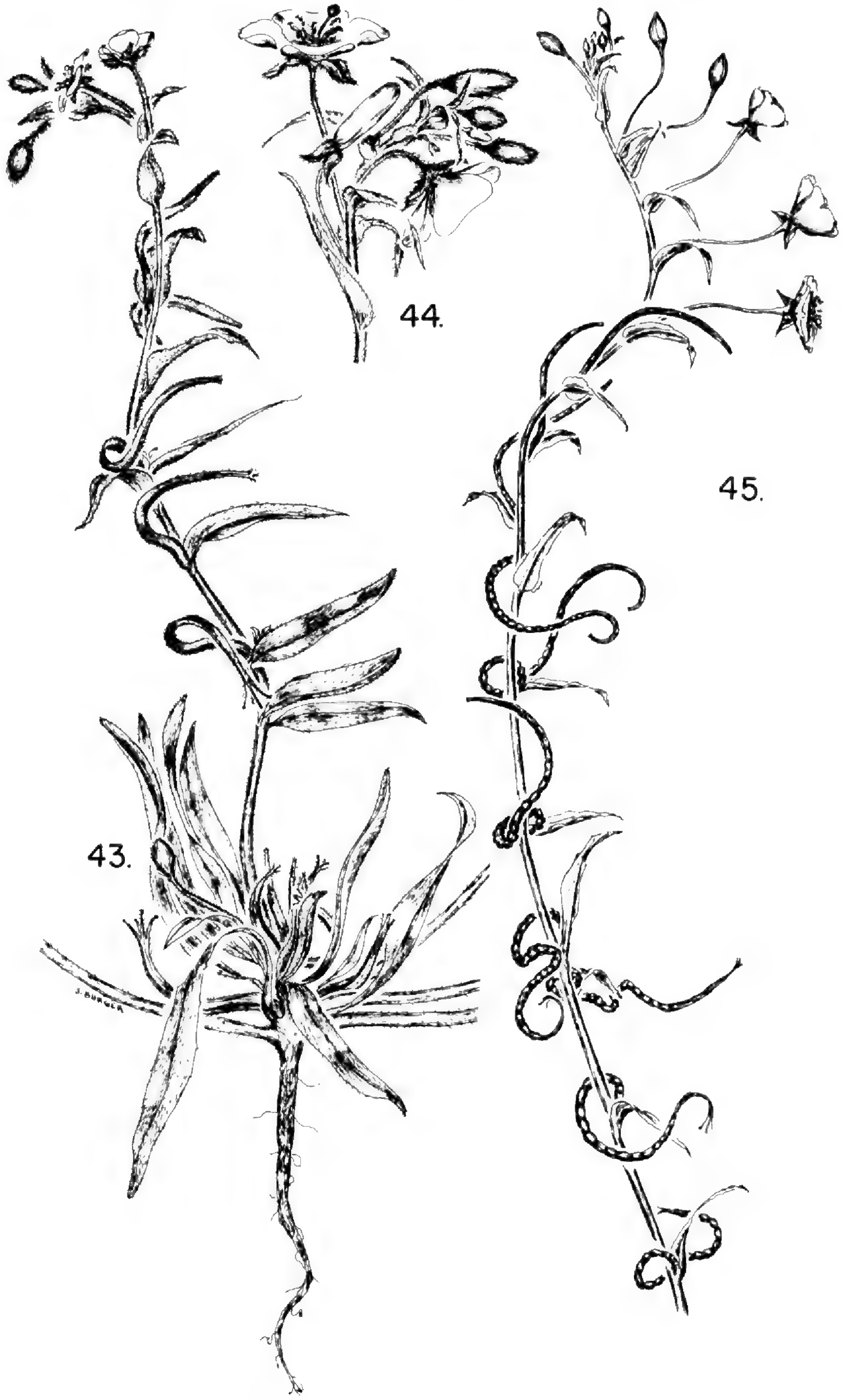
Indeed, the existence of the tetraploid populations here referred to *C. intermedia* was the primary reason that plants as different as *C. micrantha* and *C. hirtella* could ever have been referred to a single species. Serious difficulty likewise exists in separating some of the large-flowered, southern California populations of *C. hirtella* from the geographically much more restricted tetraploid *C. confusa*. *Camissonia confusa* bridges the morphological hiatus between *C. hirtella* and *C. pallida* subsp. *pallida* in the same way that the other tetraploid known in the section, *C. intermedia*, bridges the gap between *C. hirtella* and *C. micrantha*. As *C. hirtella* is sometimes more similar to *C. pallida* subsp. *pallida* than it ever is to *C. micrantha*, the taxonomic problem can be even more serious, although the vast majority of populations can be assigned to one species or the other without difficulty. The three hexaploid species in the section can readily be separated from *C. hirtella* on the basis of the proportion of 4- and 5-pored pollen grains they possess.

A single plant that was apparently a natural F_1 hybrid between *C. hirtella* and *C. ignota* was found with the two parents in Lyons Valley, 8 miles northeast of Jamul, San Diego County, California. This plant had 6 pairs of chromosomes and 2 univalents in 2 cells and 5 pairs plus 4 univalents in 3 cells at diakinesis. It appeared to have set a full complement of seeds.

33. Camissonia ignota (Jeps.) Raven, Brittonia 16: 284. 1964. FIGURE 45

Oenothera micrantha var. *ignota* Jeps., Man. Fl. Pl. Calif. 684. 1925.
Oenothera hirta var. *ignota* (Jeps.) Munz, Bot. Gaz. 85: 263. 1928.
Oenothera ignota (Jeps.) Munz, N. Amer. Fl. II. 5: 161. 1965.

Erect, often subsucculent and reddish-tinged annual, similar to *C. micrantha*, with one or more ascending branches from the basal rosette; plants to 55 cm. tall, very finely strigulose with a sparse admixture of longer trichomes. Upper leaves very narrowly to narrowly elliptic, to 6 cm. long and 1.4 cm. wide, finely serrulate, the apex acute, the base attenuate; almost all leaves evidently petiolate, the petiole up to 2.5 cm. long. Bracts truncate at base, narrowly lanceolate or lanceolate. Inflorescence subglabrous or glandular-pubescent with a few longer erect trichomes, rarely entirely strigulose. Hypanthium (1.1–) 1.8–3 mm. long, 1.1–2 mm. across at the summit, glabrous within. Sepals 2.6–5.5 mm. long, 1–1.7 mm. wide. Petals (3–) 4–8 mm. long, (2–) 3–6 mm. wide, sometimes red-dotted near the base. Filaments of the episepalous stamens (1.2–) 2.5–3.6 mm. long, those of the epipetalous ones (1–) 1.3–2 mm. long; anthers (0.6–) 0.8–1.6 mm. long. Style (3–) 4.5–7 mm. long; stigma 0.8–1.2 mm. in diameter, surrounded by the anthers at anthesis. Capsule mostly 2–3 cm. long, 0.8–1 mm. thick, terete in living material, very slender and usually much contorted, coiled irregularly up to five times, or more



FIGURES 43–45.—Species of *Camissonia* sect. *Holostigma*, × 1: 43, *C. pallida* subsp. *pallida* (*Raven* 13995, DS); 44, *C. pallida* subsp. *hallii* (*Alexander & Kellogg* 2072, DS); 45, *C. ignota* (*Raven et al.* 12524, DS).

rarely simply flexuous. Seeds 1.2–1.3 mm. long, 0.5–0.6 mm. thick. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Jurupa Hills, west of Riverside, Riverside County, California, April 1905, *Mrs. C. M. Wilder* 90 (UC 69875).

DISTRIBUTION (Figure 46): Most common in clay fields and slopes at low elevations, but occasional on sandy soil and higher in the mountains in the Coast Ranges and bordering valleys from Yolo County, California, south to the southern end of the Sierra San Miguel, at about 30° N. lat., in Baja California, usually away from the immediate coast and barely reaching the margins of the desert; Santa Cruz Island, Santa Barbara County, California; collected once in the lowest foothills of the Sierra Nevada in Madera County, California.

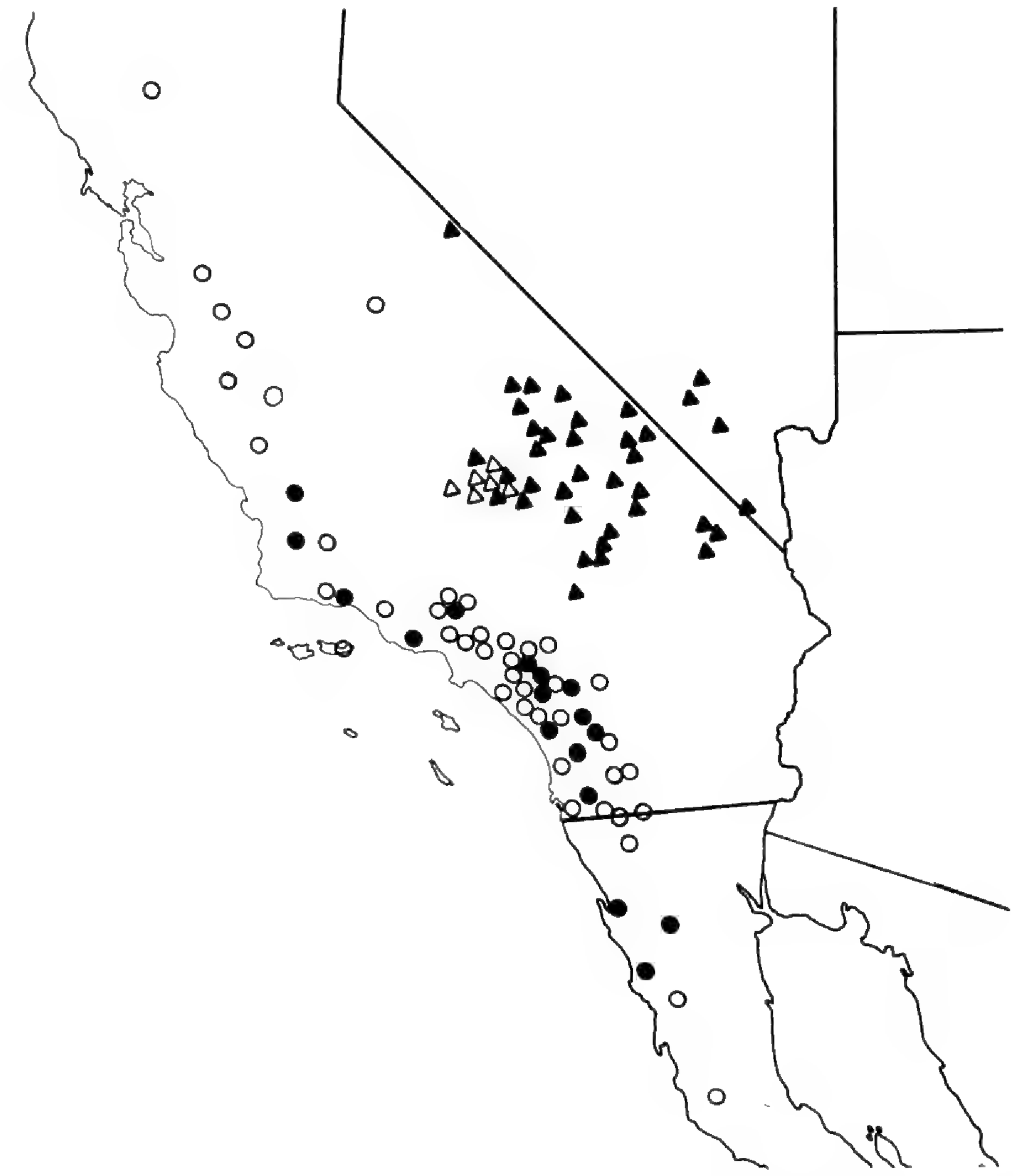


FIGURE 46.—Portion of the southwestern United States and northwestern Mexico, showing the ranges of species of *Camissonia:* ○=*C. ignota*, with ●=diploid chromosome counts ($n=7$); ▲=*C. kernensis* subsp. *gilmanii;* △=*C. kernensis* subsp. *kernensis*.

From about 400 to 3,500 ft. alt. Most abundant in western Riverside and San Diego Counties, California, and generally local and sporadic elsewhere.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: FRESNO CO.: Alcalde, *Eastwood* 13549 (CAS). LOS ANGELES CO.: 1 mi. W. of Acton, Soledad Canyon, *Lewis* in 1954 (LA); 3 mi. S. of Boquet Canyon Guard Station, *Tavares & Brinson* 263 (DAO, RM, SD, UC); San Fernando wash, *Eastwood* in 1913 (CAS); Tujunga Canyon, 1,500 ft., *Peirson* 414 (JEPS, RSA); Griffith Park, *Davidson* 1451 (LAM); San Dimas Canyon, 1,500 ft., *Harwood* 3692 (POM); Johnson's Pasture, 3 mi. N. of Claremont, *Jones* in 1928 (CAS). MADERA CO.: San Joaquin R. ca. 5 mi. above Pollasky, *Heller* 8166 (CAS, DS, F, GH, NY, PH, UC, US). MERCED CO.: Ortigalita Peak, San Carlos Range, *Lyon* 1529 (RM, UC, WTU); Pacheco Pass, *Eastwood* 14092 (CAS). MONTEREY CO.: Lowes Canyon, *Hardham* 3317 (CAS, LA). ORANGE CO.: Trail to Santiago Peak from Trabuco Canyon, in Holy Jim Canyon, 3,500 ft., *Peirson* 3505 (RSA); 2.3 mi. above gate on Silverado Canyon Truck Trail, 2,500 ft., R17750 (DS); Anaheim plains, *King* in 1908 (JEPS). RIVERSIDE CO.: Temescal Canyon, ca. 12 mi. SE. of Corona, *Hitchcock & Muhlick* 22151 (DS, RM, UC, UT, WTU); Elsinore, *McClatchie* in 1892 (DS, NY); Temecula, *Cleveland* in 1882 (SD); Coldwater Trail, Santa Ana Mts., *Pequegnat* 2 (LA); Rattlesnake Mts., *Wilder* in 1905 (DS); Saunders Meadow, *Meyer* 161 (JEPS). SAN BENITO CO.: Pinnacles, *Sutliffe* in 1920 (CAS). SAN BERNARDINO CO.: Vicinity of San Bernardino, *Parish* 4756 (NY, US); near Colton, *Parish* 78 (DS, UC). SAN DIEGO CO.: Moro Hills near Fallbrook, *Abrams* 3326 (CAS, DS, GH, LA, LE, NY, PH, POM, UC, US); 2.3 mi. S. of Rincon Springs on road to Escondido, 1,100 ft., R17402 (DS); 1 mi. E. of Oak Grove, 2,700 ft., R17370 (DS); 2 mi. W. of Banner, *Gander* 173.3 (SD); Barrett, R16936 (DS); 1.1 mi. E. of Campo, R17445 (DS); Jacumba, *Gander* 181.6 (SD). SAN LUIS OBISPO CO.: Upper Navajo Creek, La Panza Range, *Hoover* 6904 (CAS, RSA); Cuyama Valley 44 mi. W. of Maricopa, 2,000 ft. *Benson* 5787 (POM). SANTA BARBARA CO.: Santa Ynez Mts., *Eastwood* in 1904 (CAS); Valley Anchorage, Santa Cruz I., *Hoffmann* in 1929 (POM). STANISLAUS CO.: Near head of Del Puerto Canyon, *Hoover* 4883 (UC). VENTURA CO.: Burn near Kennedy Canyon, Ojai Valley, *Pollard* in 1946 (RSA). YOLO CO.: Grade on Rumsey to Arbuckle road, *Hoover* 3199 (POM, RSA, UC, US).

Camissonia ignota as here constituted is, in general, a very distinctive entity that includes most of the populations referred by Munz (Bot. Gaz. 85: 263. 1928) to *Oenothera hirta* var. *ignota* and later to *Oenothera micrantha* var. *ignota*. Many of the populations here considered to belong to the tetraploid *C. confusa* were considered by Munz to belong to this taxon also. These differ in their more robust habit, broader leaves, abundant gray pubescence, less contorted capsules, and tetraploid chromosome number. At times, however, the separation of *C. confusa* from *C. ignota* can be very difficult, and it is not impossible that *C. ignota* has contributed to the origin of some of the tetraploid populations I have included with *C. confusa*. In general, however, it appears more probable that the diploid parents of the latter species are *C. hirtella* and *C. pallida* subsp. *pallida*. It does not appear likely that *C. ignota* has contributed to the formation of any

other polyploid species, although at one time I thought that the tetraploid Baja California populations here referred to *C. intermedia* might have been derived from the diploids *C. proavita* and *C. ignota* (see discussion under *C. intermedia*). The chromosome number of *Camissonia ignota* has been determined in 22 individuals taken from 18 populations from throughout the range (see Appendix).

Camissonia ignota has been observed growing sympatrically with *C. bistorta, C. lewisii, C. proavita, C. hirtella, C. intermedia,* and *C. confusa.* A single F_1 hybrid with *C. hirtella* was found in San Diego County, California, and is discussed under that species.

34. Camissonia pallida (Abrams) Raven, Brittonia 16: 284. 1964.

Similar to *C. micrantha,* but covered with dense, strigose pubescence. Leaves entire or very sparsely denticulate, the upper ones undulate, mostly 1–3 cm. long, 0.35–0.7 cm. wide, with a short but distinct petiole up to 2 mm. long. Inflorescence occasionally with an admixture of glandular trichomes, usually conspicuously gray-pubescent. Hypanthium (1–) 1.8–4 mm. long, (0.7–) 1.2–3.5 mm. across at the summit. Sepals (1.5–) 2.5–8 mm. long, 0.6–3 mm. wide. Petals (2–) 3.5–13 mm. long, (1.3–) 3–14.5 mm. wide, occasionally with 1–3 red dots near the base. Filaments of the episepalous stamens (0.5–) 1.5–6.5 mm. long, those of the epipetalous ones (0.2–) 0.5–3.8 mm. long; anthers (0.4–) 0.8–2.2 mm. long. Style (2–) 3–10.5 mm. long; stigma 0.6–1.5 mm. in diameter, surrounded by at least the anthers of the longer stamens and often by both sets of anthers at anthesis. Capsule 1–1.2 mm. thick, more or less quadrangular in transection, straight or once or more coiled, rarely up to three times. Seeds 1–1.45 mm. long, 0.6–0.7 mm. thick. Gametic chromosome number, $n=7$. Autogamous.

Distribution (Figures 33, 42): Desert slopes and flats, often along washes, from the head of the San Joaquin Valley in Ventura and Kern Counties, California, across the Mojave and Colorado Deserts, north to the vicinity of Independence, Inyo County, California, and Esmeralda County, Nevada (the only member of the section in Nevada); east to Mohave and Yavapai Counties, Arizona, and also in the vicinity of Tucson, Pima County; and south along the eastern side of Baja California to the Sierra de San Borjas at about 29° N. lat.; from about 100–6,000 ft. alt.

Camissonia pallida consists of two subspecies: subsp. *hallii,* which is relatively large-flowered, and subsp. *pallida.* The former occupies a much more restricted range than the latter, and often grows with it. Numerous intermediate individuals are found in such localities, and the plants appear to differ only in flower size. No meiotic disturbances or evidences of sterility have been found in individuals with intermediate-sized flowers. Presumably the distinctness of these two

species is maintained by their predominant autogamy. *Camissonia pallida* subsp. *hallii* was considered a variety of *Oenothera bistorta* (=*Camissonia bistorta*) by Munz (Bot. Gaz. 85: 267. 1928). Despite their similarity in flower size, however, *C. bistorta* is self-incompatible and the stigma is elevated above the anthers at anthesis, whereas *C. pallida* subsp. *hallii* is autogamous, the anthers shedding pollen directly on the stigma at anthesis. Vegetatively, these two entities are sharply distinct.

34a. Camissonia pallida subsp. **hallii** (Davids.) Raven, Brittonia 16: 284. 1964. FIGURE 44

Sphaerostigma hallii Davids., Muhlenbergia 3: 107. 1907.
Oenothera bistorta var. *hallii* (Davids.) Jeps., Man. Fl. Pl. Calif. 685. 1925.
Oenothera hallii (Davids.) Munz, N. Amer. Fl. II. 5: 160. 1965.

Hypanthium 3.8–4.2 mm. long, 2.2–3.5 mm. across at the summit. Sepals 4.8–8 mm. long, 1.2–3 mm. wide. Petals 6.5–13 mm. long, 5–14.5 wide, with 1–3 red dots near the base of each one. Filaments of the episepalous stamens 3–6.5 mm. long, those of the epipetalous ones 1.8–3.8 mm. long; anthers 1.5–2.2 mm. long. Style 6.5–10.5 mm. long, the longer stamens just equal to and their anthers shedding pollen directly on the stigma at anthesis. Gametic chromosome number, $n=7$. Autogamous, but clearly facultatively outcrossing.

TYPE: Banning, Riverside County, California, 17 April 1897, *H. M. Hall* 446 (UC).

DISTRIBUTION (Figure 33): Sandy washes in Riverside and San Bernardino Counties, California, ca. 100–4,300 ft. alt., from Banning east throughout the Little San Bernardino Mountains and their northern slopes and southeast to the vicinity of Mecca and Box Canyon.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S: CALIFORNIA: RIVERSIDE CO.: Big Oaks Canyon, Banning, 4,000 ft., *Cooper* 1645 (RSA); Whitewater Canyon 2 mi. N. of Banning-Indio boulevard, *Munz* 15660 (CAS, DS, GH, POM, UC, US, WS, WTU); near Mecca, *Winblad* in 1937 (CAS); Box Canyon, *Winblad* in 1937 (CAS). SAN BERNARDINO CO.: Just S. of Morongo Valley, 2,600 ft., R17532 (DS); E. of Quail Spring, *Moran* 844 (DS, POM, UC).

Camissonia pallida subsp. *hallii* has not been observed growing sympatrically with any other member of the section, except *C. pallida* subsp. *pallida*, with which it intergrades. Its chromosome number has been determined in 4 individuals from 3 different populations (see Appendix). The combination *Camissonia hallii*, attributed to me by Munz, N. Amer. Fl. II. 5: 160. 1965, has not been published elsewhere.

Relatively large-flowered plants similar to subsp. *hallii* are occasionally found elsewhere in the area of subsp. *pallida*. One such collection was made in the pinyon-juniper association of the Cerbat Mountains,

Mohave County, Arizona, 5,000 ft. elevation, *Jaeger* in 1941 (POM); the petals of one plant are 11.5 mm. long and 8 mm. wide, and have red dots near the base similar to those usually found in subsp. *pallida*. One of the plants mounted on this sheet is typical of subsp. *pallida*, with petals ca. 3.5 mm. long. It would be highly desirable to have more material for study before extending the range of subsp. *hallii* to this disjunct station.

34b. Camissonia pallida subsp. **pallida** FIGURE 43

Sphaerostigma pallidum Abrams, Bull. Torrey Cl. 32: 539. 1905.

Sphaerostigma micranthum var. *exfoliatum* A. Nels., Bot. Gaz. 40: 59. 1905. Lectotype: Colorado Desert, probably in San Diego Co., Calif., April 1889, *C. R. Orcutt*.

Oenothera abramsi J. F. Macbride, Contr. Gray Herb. 65: 41. 1922.

Oenothera micrantha var. *abramsii* (J. F. Macbride) Jeps., Man. Fl. Pl. Calif. 684. 1925.

Oenothera hirta var. *exfoliata* (A. Nels.) Munz, Bot. Gaz. 85: 264. 1928.

Oenothera micrantha var. *exfoliata* (A. Nels.) Munz, Amer. Journ. Bot. 19: 778. 1932.

Hypanthium (1–) 1.8–3 mm. long, (0.7–) 1.2–2.5 mm. across at the summit. Sepals (1.5–) 2.5–5.5 mm. long, 0.6–2 mm. wide. Petals (2–) 3.5–6 (–8) mm. long, (1.3–) 3–5 (–6.5) mm. wide, very rarely with red dots at the base. Filaments of the episepalous stamens (0.5–) 1.5–4 mm. long, those of the epipetalous ones (0.2–) 0.5–2.2 mm. long; anthers (0.4–) 0.8–1.2 mm. long. Style (2.1–) 3–6.5 mm. long, the stigma surrounded at anthesis by both sets of anthers, or sometimes by only the longer set. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Near the station, Cabazon, Riverside County, California, 6 April 1903, *L. R. Abrams* 3228 (NY; isotypes, CAS, DS, GH, LA, LE, NY, RM, RSA, SBM, UC, US, WS, WTU).

DISTRIBUTION (Figure 42): That of the species.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: ARIZONA: MOHAVE CO.: 9 mi. NW. of Kingman, 3,300 ft., *Munz et al.* 22982 (DAO, RSA, UC). PIMA CO.: Bear Canyon, Santa Catalina Mts., *Mason et al.* in 1960. YAVAPAI CO.: 5.4 mi. NE. of Congress, 4,000 ft., R17367 (DS); Skull Valley, 4,300 ft., *Jones* in 1903 (POM). CALIFORNIA: IMPERIAL CO.: 0.5 mi. E. of Mountain Springs, *Ferris* 7078 (DS, NY). INYO CO.: North Fork of Oak Creek, Independence, 3,000 ft., *Train* in 1937 (ARIZ, DS, OSC); 2.5 mi. E. of Coso Hot Springs, Coso Range, 3,550 ft., *Alexander & Kellogg* 2768 (UC). KERN CO.: S. end of Soledad Mt., 2,775 ft., *Twisselmann* 4308 (CAS, LA); 9.7 mi. S. of Weldon, 3,100 ft., R17565 (DS); Poso Creek, slope on S. side, Greenhorn Mts., ca. 2,600 ft., *Smith* 299 (JEPS). LOS ANGELES CO.: N. of Pearblossom, *Wedberg* 250 (DS); 2 mi. N. of Saugus, *Munz* 10013 (POM, UC); Rock Creek to Big Pines, 4,500 ft., *Pierson* 7951 (RSA). RIVERSIDE CO.: Dos Palmos Spring, N. end of Santa Rosa Mts., 3,600 ft., *Munz* 15107 (CAS, GH, POM, UC); San Gorgonio Pass, 1 mi. W. of Whitewater, 1,200 ft., *Wolf* 8416 (ARIZ, GH, NY, RSA, WTU); Palm Canyon near Palm Springs, *Johnston* 1110 (DS, POM, US); Indio, *McGregor* in 1917 (DS); Fried Liver Wash, Pinto Basin, Joshua Tree

National Monument, R11863 (DS); 5 mi. S. of Gold Coin Mine, Little San Bernardino Mts., *Epling & Robinson* in 1933 (DS, LA, RSA). SAN BERNARDINO co.: Cedar Canyon, Mid Hills, 5,000 ft., R17353 (DS); 3.5 mi. N. of Lake Arrowhead, 4,550 ft., *Axelrod* 273 (UC); Cajon Pass, 3,800 ft., *Jones* in 1903 (POM); Cactus Flat, San Bernardino Mts., 6,000 ft., *Munz* 10518 (POM); Granite Mts., N. of Amboy, *Jaeger* in 1939 (DS). SAN DIEGO co.: Hell Hole Canyon, Borrego Valley, *Epling & Robinson* in 1932 (DS, F, LA, NY, RSA, UC); extreme SE. corner of the county, *Gander* in 1940 (SD); 11 mi. E. of Banner, *Gould* 2268 (RSA, UC); 5 mi. E. of Laguna Station, 1,090 m, *Bracelin* 5 (POM, UC). VENTURA co.: Flood plain of Piru Creek, *Hoffmann* in 1930 (CAS, SBM); sandy field near Camulos, *Hoffmann* in 1929 (SBM). NEVADA: ESMERALDA CO.: 2 mi. E. of Bellville, *Purpus* in 1898 (UC).

BAJA CALIFORNIA. Vicinity of Japá, *Orcutt* 1191 (UC); 3 mi. W. of Santa Catarina, 64 mi. SE. of Ensenada, 3,755 ft., *Broder* 659 (DS, UCSB); Rancho San Matias, Sierra San Pedro Mártir, ca. 1,050 m, *Moran* 10844 (DS, SD); San Juan Mine, Sierra de San Borjas, ca. 1,200 m, *Moran* 8127 (RSA, SD, UC).

This extraordinarily variable taxon is at times difficult to separate from *C. hirtella* where the ranges of these two species approach one another along the margins of the desert. There is, however, no evidence of genuine intergradation, and most plants are easily referred to one species or the other. An even more difficult problem is the separation of *C. pallida* subsp. *pallida* from *C. confusa*, which is presumably an allotetraploid derived from the diploids *C. pallida* subsp. *pallida* and *C. hirtella*. In California, the problem is rarely a difficult one, but in Arizona further chromosome counts will clearly be necessary to elucidate the situation completely. All collections from the area of the Tonto National Forest in Gila and Maricopa Counties appear to be *C. confusa*, and this is documented by chromosome counts from the area. Collections from Paradise Valley and Avondale, farther west in Maricopa County, and the vicinity of Sacaton and Casa Grande Ruins, to the south in Pinal County, also are morphologically similar to the tetraploids of California. Populations in Yavapai and Mohave Counties, on the other hand, are known to be diploid. A series of populations from the vicinity of Tucson and the Santa Catalina Mountains in Pima County, Arizona, appears morphologically similar to the diploid and are tentatively referred here, even though they would, if this disposition is correct, represent a disjunct occurrence for *C. pallida* subsp. *pallida*. Unfortunately none of these populations has been examined cytologically.

The chromosome number of this subspecies has been determined in 26 individuals from 24 populations scattered throughout the range (see Appendix). *Camissonia pallida* subsp. *pallida* intergrades with *C. pallida* subsp. *hallii* and occurs sympatrically with *C. hirtella* and probably *C. ignota* (the latter in the vicinity of Santa Catarina, Baja California).

35. Camissonia intermedia Raven, sp. nov. FIGURE 48

Oenothera hirta var. *typica* sensu Munz, Bot. Gaz. 85: 261, 1928; pro parte.
Oenothera hirta var. *jonesii* sensu Munz, Bot. Gaz. 85: 262. 1928; pro parte.
Oenothera micrantha sensu Munz, N. Amer. Fl. II. 5: 160. 1965; pro parte.

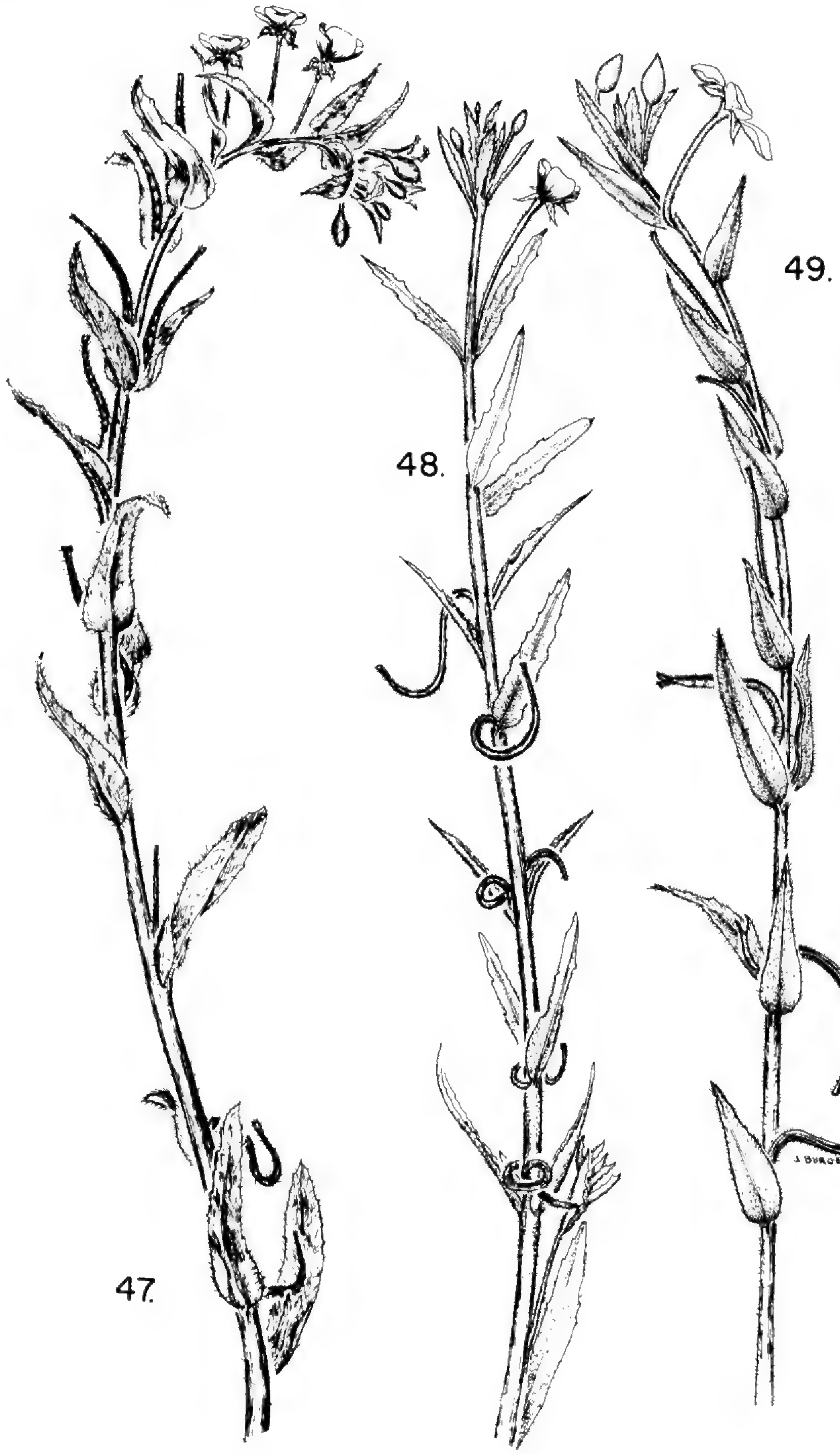
Herba annua dense villosa erecta, ad *C. micrantha* similis, usque ad 6 dm alta, ramis plurimis erectis e rosula centrali radiantibus, rariore caule singulari erecto. Folia his *C. micranthae* basi parum latiora. Inflorescentia plus minusve cano-villosa, persaepe pilis brevibus glandulosis pubescentes. Usque ad partem vicensimam pollinis granorum quadriporam, rariore ad partem dimidiam. Chromosomatum numerus gameticus, $n=14$. Autogama.

TYPE: Common along disturbed roadsides in chaparral, with *Adenostoma fasciculatum* and *Arctostaphylos glauca*, Mulholland Highway 2.6 miles east of Seminole Hot Springs, 1,800 ft. alt., Santa Monica Mountains, Los Angeles County, California, 1 May 1962, *P. H. Raven* 17517 (DS 514938; isotypes, RSA, US).

DISTRIBUTION (Figure 50): Mostly on disturbed brushy slopes, often common on burns, from Lake and Yolo Counties (where rare) south in the Coast Ranges of California to the western San Gabriel Mountains, western Riverside County, and San Diego County, and south in Baja California to the south end of the Sierra San Miguel at about 30° N. lat.; also on Santa Cruz and Santa Catalina Islands. From (500–) 1,000–2,500 ft. alt. Most abundant in Monterey County and from coastal Santa Barbara County to the Santa Monica Mountains of Los Angeles and Ventura Counties, California, and again in coastal Baja California.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: CONTRA COSTA CO.: W. slope of Mt. Diablo, ca. 900 ft. *Rose* 41229 (GH, NY, UC). LAKE CO.: Blue Lakes, *Baker* 264a (DS). LOS ANGELES CO.: Wilson's Trail, *Abrams* 1505 (DS); foothills near Sherman, *Braunton* 65 (US); Puddingstone Canyon, *Munz et al.* 2444 (POM); Liveoak Canyon Dam, San Gabriel Mts., 1,500 ft., *Wheeler* 2543 (LA); Mandeville Canyon, 1,200 ft., Santa Monica Mts., *Templeton & Clokey* 4458 (DAO, NY, POM, UC, US); Los Alisos Canyon, Santa Monica Mts., *Epling* in 1931 (CAS, F, LA, UC, US); Avalon Hill, Santa Catalina I., *Knopf* 428 (F). MONTEREY CO.: Priest Valley, 2,250 ft., *Howell* 39114 (CAS); limestone ridge above Posts, ca. 2,000 ft., Big Sur, *Hoffman* 1180 (UC). NAPA CO.: Oakville to Glen Ellen, ca. 900 ft., R2860 (CAS); Capell Valley, *Kamb & Chisaki* 1760 (UCSB). ORANGE CO.: Santiago Peak Trail, *Abrams* 1792 (NY); 5 mi. S. of Laguna, *Mason* 2926 (UC). RIVERSIDE CO.: 5 mi. NE. of Murietta, 1,500 ft., *Munz & Johnston* 5354 (POM). SAN BENITO CO.: 10.5 mi. from junction near Bitterwater on road to Hernandez, R9152 (CAS, LA, RSA, UC); Bear Valley, *Jepson* 12246 (JEPS). SAN DIEGO CO.: Near County line on U.S. Hwy. 395, *Gander* in 1937 (SD); Jamul, 1,500 ft., *Stokes* in 1895 (DS). SAN LUIS OBISPO CO.: Chimney Ranch, North Road to Adelaida, *Hardham* 3347 (LA, SBBG); east School Canyon, San Luis Obispo, *Condit* in 1908 (UC). SANTA BARBARA CO.: N. of Lompoc, *Chandler* 2570 (DS); Los Feliz School at end of Mission Canyon Road, 1,000 ft., *Smith* 920 (RSA); Gibraltar Road to El Camino



FIGURES 47–49.—Species of *Camissonia* sect. *Holostigma*, × 1: 47, *C. hardhamiae* (*Raven* 18315, holotype, DS); 48, *C. intermedia* (*Breedlove* 2305, DS); 49, *C. luciae* (*Raven* 18267, holotype, DS).

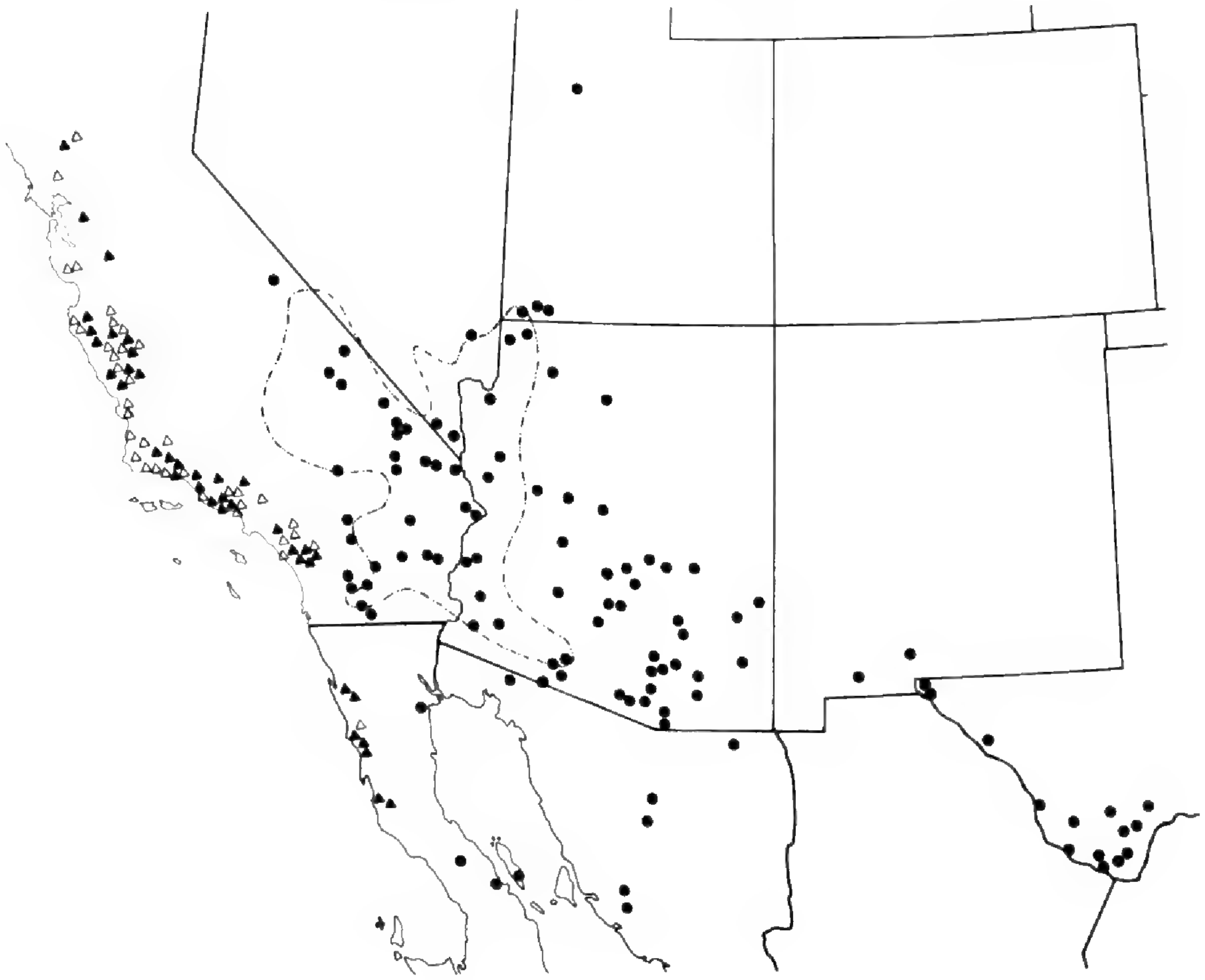


FIGURE 50.—Portion of the southwestern United States and northwestern Mexico, showing the ranges of species of *Camissonia:* △=*C. intermedia*, with ▲=tetraploid chromosome counts (*n*=14); ●=*C. chamaenerioides;* the dotted-line outline indicates the range of the related, larger flowered, self-incompatible *C. refracta*.

Cielo, 2,000 ft., *Hardham* 10854 (DS); Sierra Blanca, Santa Cruz I., *Wolf* 2842 (POM, RSA); Coches Prietos Canyon to Alberts Anchorage, 400 ft., top of ridge, *Blakley* 3314 (SBBG). SANTA CLARA CO.: Evergreen, *Burtt Davy* 71 (UC); Loma Prieta, *Burtt Davy* 665 (UC). SANTA CRUZ CO.: Near summit of Santa Cruz to Los Gatos highway, *Covel* 323 (CAS). STANISLAUS CO.: Near head of Del Puerto Canyon, *Hoover* 4884 (RSA, UC). VENTURA CO.: Santa Susanna Pass, *Epling* in 1926 (LA); Foster Park burn, Ojai Valley, *Pollard* in 1945 (CAS, RSA, SBM). YOLO CO.: Grade on Rumsey-Arbuckle road, *Hoover* 3195 (POM, RSA, UC).

BAJA CALIFORNIA: 10 mi. S. of Ensenada, *Purer* 7140 (SD); near San Jacinto, *Gander* in 1939 (SD); near Refugio, *Cronemiller* 3083 (POM); 13.1 mi. S. of Santo Tomás, *Turner et al.* 2074 (DS); 9.3 mi. S. of San Vicente, R17045 (DS); 2.5 mi. S. of Ejido México, R17039 (DS).

Camissonia intermedia is almost certainly an allotetraploid, its two diploid ancestors being *C. micrantha* and *C. hirtella*. The difficulties of distinguishing it from these two diploids have been discussed in the sections dealing with each. At one time, I thought that the tetraploid populations of Baja California here referred to *C. intermedia* might have been derived from the diploids *C. ignota* and *C. proavita*, as mentioned under the latter species. Evidence for

this view is the fact that *C. micrantha*, one of the parents of the northern populations of *C. intermedia*, ranges no farther south than northern San Diego County, California, where the main area of the tetraploid stops also. No tetraploids have been found in central San Diego County, despite intensive sampling, and the Baja California populations range north only to Jamul in the southernmost part of the county. In general, the plants found in Baja California seem to be somewhat more slender and glabrous than the ones from farther north; but this is far from an absolute difference, and I have found it difficult to quantify. It might be possible to elucidate this problem with a program of experimental hybridization, but at present it appears best to retain all of these obviously closely related tetraploid populations in a single species.

The chromosome number of this species has been determined in 60 individuals from 53 populations from throughout the range of the species including the type (see Appendix). *Camissonia intermedia* has been found growing sympatrically with *C. bistorta*, *C. lewisii*, *C. proavita*, *C. micrantha*, *C. hirtella*, *C. ignota*, *C. confusa*, and *C. robusta*. Individuals of this species were referred by Munz (Bot. Gaz. 85: 260–265. 1928) to *Oenothera hirta* var. *typica* and *O. hirta* var. *jonesii*, entities corresponding for the most part to the diploid parents of *C. intermedia*.

36. Camissonia confusa Raven, sp. nov. FIGURE 51

Oenothera hirta var. *ignota* sensu Munz, Bot. Gaz. 85: 263. 1928; pro parte.
Oenothera ignota sensu Munz, N. Amer. Fl. II. 5: 161. 1965; pro parte.

Herba annua robusta dense cinerero-villosa rare strigosa erecta, ad *C. micrantha* similis, usque ad 6 dm. alta, ramis plurimis erectis e rosula centrali radiantibus, rariore caule singulari erecto. Folia superiora lanceolata vel anguste ovata, 1–5 cm. longa, 0.4–2 cm. lata, basi rotundata vel truncata, sparse et exigue denticulata, undulata, apice longe acuminata. Inflorescentia glandulosa, rariore pilis longioribus admixta vel strigosa, rarissime subglabra. Hypanthium (1.8–) 2–3.8 mm. longum, ostio 1.2–2 mm. diametro. Sepala (1.5–) 3.2–8.5 mm. longa, 1.2–1.5 mm. lata. Petala (2.5–) 5–10.5 mm. longa, (1.5–) 2.8–6 mm. lata, plerumque prope basin puncto rubro uno vel duo. Filamenta staminum episepalorum (1.2–) 2.5–4.5 mm. longa, illa epipetalorum (0.8–) 1.5–2.5 mm. longa; antherae (0.4–) 0.8–1.5 mm. longae. Usque ad partem vicensimam pollinis granorum quadriporum. Stylus (2.5–) 4.5–7.5 mm. longus; stigma 1–1.2 mm. diametro, sub anthesi antheris saltem longioribus circumnexum. Capsula 0.9–1.2 mm. crassa surrecta vel in spiras 1 vel 2 contorta. Semina 1.2–1.35 mm. longa, 0.5–0.7 mm. crassa. Chromosomatum numerus gameticus, $n=14$. Autogama.

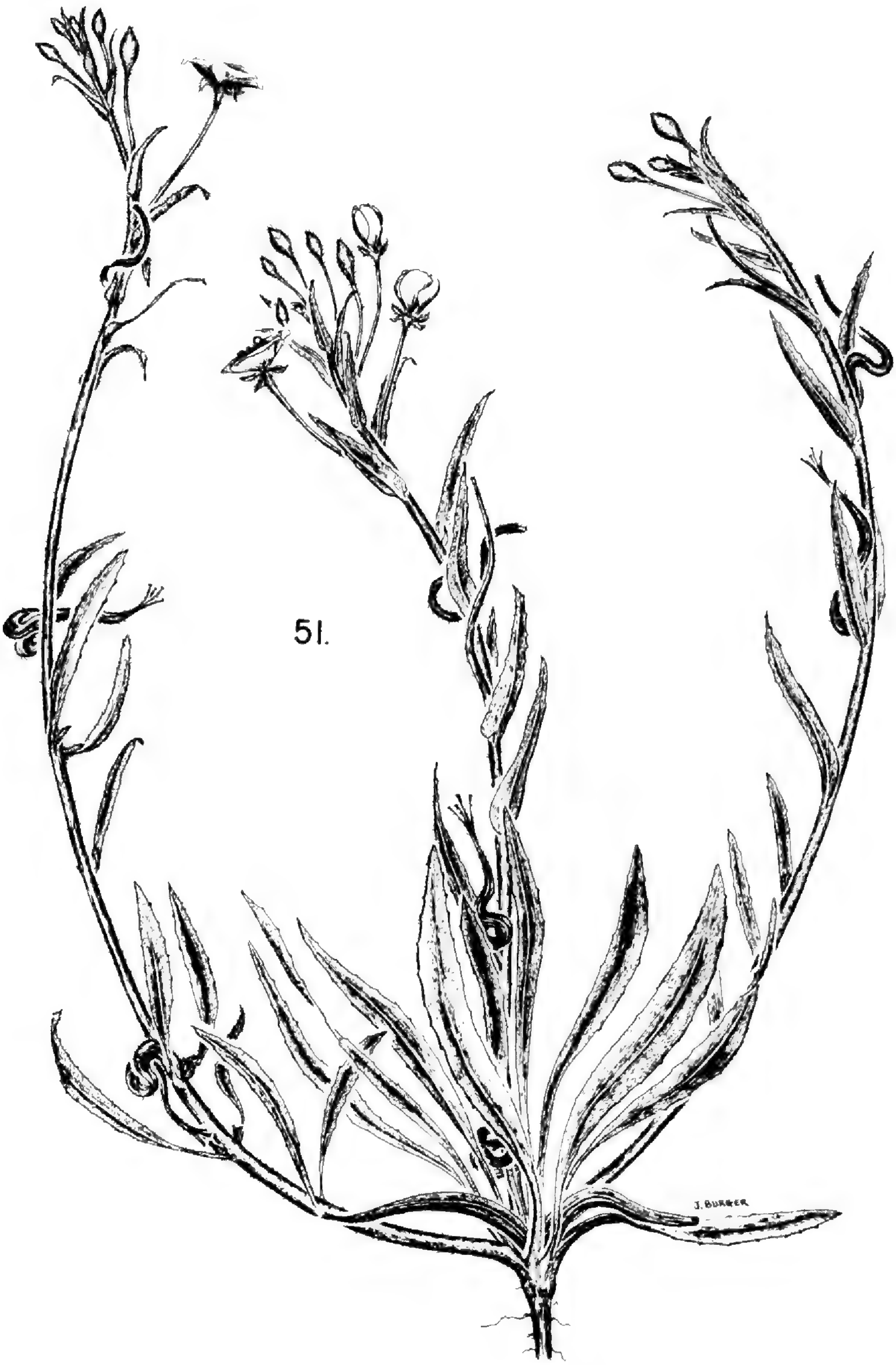


FIGURE 51.—*Camissonia confusa* (*Raven* 17388, DS), × 1.

TYPE: Common in coastal sage by edge of citrus orchard, along dirt road 2.3 miles west of Mill Creek Ranger Station, San Bernardino Mountains, 2,300 ft. alt., San Bernardino County, California, 28 April 1962, *P. H. Raven* 17466 (DS 515446; isotypes, RSA, US).

DISTRIBUTION (Figure 52): Dry slopes away from the coast, from the La Panza Range of central San Luis Obispo County south through the Coast Ranges to the San Bernardino Mountains and southern San Diego County, California; also in central Arizona (westernmost Gila, northern Pinal, and Maricopa Counties); from about 1,100–6,600 ft. alt.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: ARIZONA: GILA CO.: Tonto Hill, 690 m., *Collom* 265 (GH, NY); 12 mi. N. of Roosevelt, 2,300 ft., *Peebles & Smith* 11503 (ARIZ); Jana Gordo Wash, 1,800

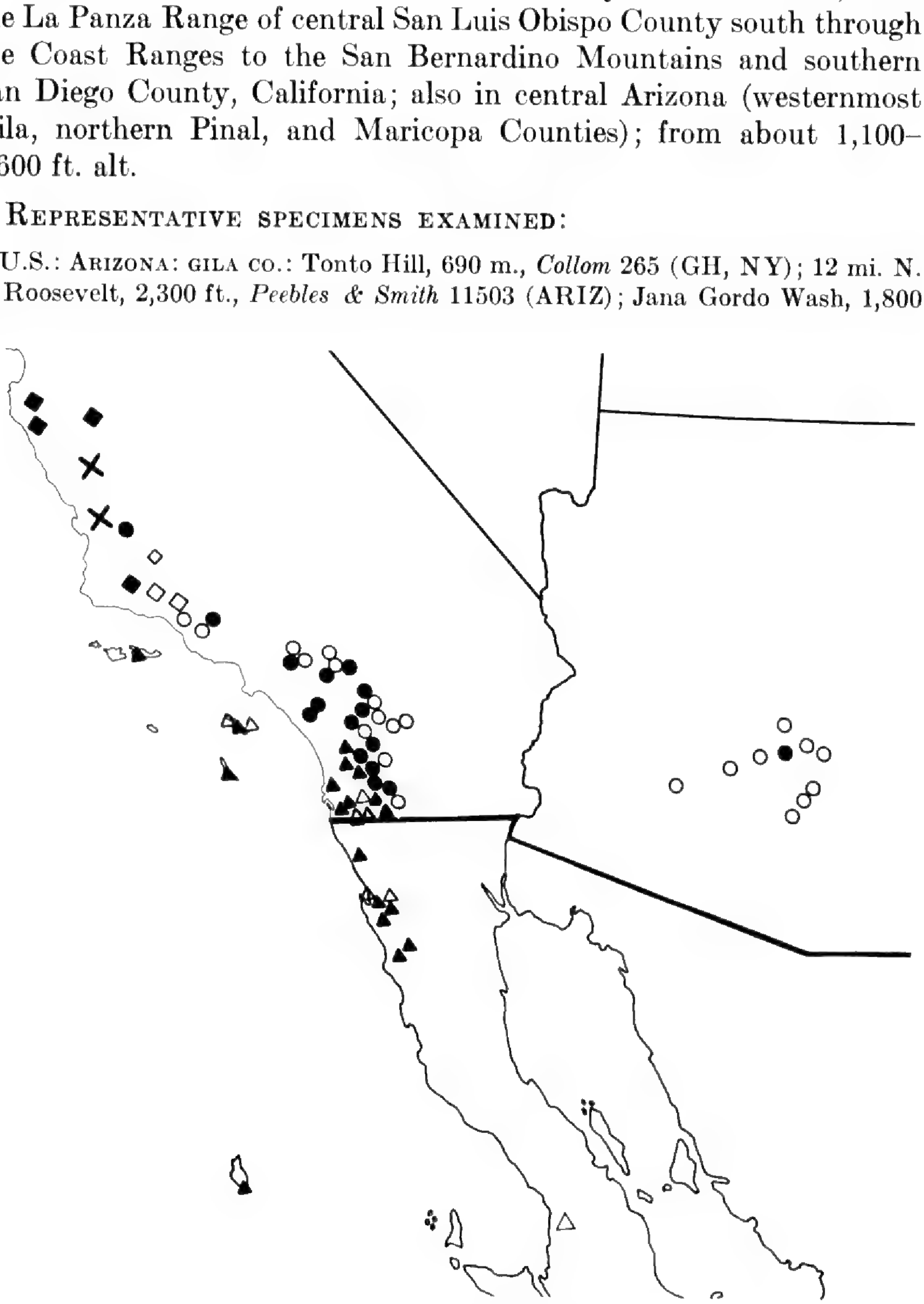


FIGURE 52.—Portion of the southwestern United States and northwestern Mexico, showing the ranges of species of *Camissonia* sect. *Holostigma:* ○=*C. confusa*, with ●=tetraploid chromosome counts (*n*=14); ×=*C. hardhamiae;* ◇=*C. luciae*, with ◆=hexaploid chromosome counts (*n*=21); △=*C. robusta*, with ▲=hexaploid counts (*n*=21).

ft., *Wittbank* 143 (US); Collom Camp, Mazatzal Mts., 1,200 m, *Collom* 268 (ARIZ, US). MOHAVE CO.: Tempe, *Gamong & Blaschke* in 1892 (US); 12.1 mi. SW. of Roosevelt on State Hwy. 88, 2,300 ft., *Gregory* 60B (DS, RSA, UC); Oak Flats, mountains between Miami and Superior, *A. & R. A. Nelson* 1858 (K, RM); 6 mi. SW. of Superior, *Russell* 11271 (OSC); Paradise Valley, 25 mi. N. of Phoenix, *Peebles et al.* 5102 (ARIZ, US); 25 mi. E. Scottsdale on Beeline Hwy., 1,160 ft., *Kennedy* 98 (DS); on canyon road 12 mi. from Apache Lodge, *Eastwood* 17161 (CAS). PINAL CO.: Superstition Mt., *Beckett* 10784 (ARIZ); Sacaton, *Peebles & Harrison* 1759 (US); sandy washes of the Gila R. near Casa Grande Ruins, *A. & R. A. Nelson* 1677 (RM). CALIFORNIA: ORANGE CO.: Lower San Juan Campground, *Bates* 2318 (DS). RIVERSIDE CO.: 3.6 mi. NE. of Aguanga, *Vestal* 63113.8 (DS); Main Divide Truck Trail at Ortega Hwy., Santa Ana Mts., 2,300 ft., R17763 (DS); ca. 4 mi. E. of Redlands, *Klein et al.* 265 (DS); 10 mi. S. of Hemet, *Munz* 10819 (POM, SBM); 18 mi. from Banning on road to Idyllwild, 5,000 ft., *Munz* 8142 (GH, POM). SAN BERNARDINO CO.: Oak Glen, *Munz & Hitchcock* 10916 (GH, POM); San Antonio Canyon, San Gabriel Mts., 5,500 ft., *Peirson* 2706 (POM, RSA); N. of Upland, *Breitung* 15060 (DAO); foothills, San Bernardino Mts., *Parish* in 1891 (NY). SAN DIEGO CO.: 3.1 mi. from U.S. Hwy. 80 on road to Morena L., 3,400 ft., R17439 (DS); Banner, *Keck et al.* 6089 (NY); 1 mi. E. of Warners Ranch, 3,400 ft., *McCully* 19 (POM); 6 mi. N. of Santa Ysabel, *Munz* 9808 (POM).

Camissonia confusa is a rather rare allotetraploid species which can readily be confused with certain populations of either of its presumed diploid parents, *C. hirtella* and *C. pallida* subsp. *pallida*. The problems of separating it from its two putative ancestors have been discussed under the treatments of the diploids, and it should be reemphasized at this point that further chromosome counts are badly needed from Arizona. As mentioned in the treatment of *C. ignota*, many of the collections of *C. confusa* have been confused with that diploid entity, and it is possible that *C. ignota* may have participated in the origin of some of the tetraploid populations here referred to *C. confusa*.

The chromosome number of *C. confusa* has been determined in 29 individuals from 22 populations, including the type collection (see Appendix). It has been observed growing sympatrically with *C. bistorta, C. micrantha, C. hirtella, C. ignota* and *C. intermedia*. North of San Bernardino County, California, populations are very scattered, but the following collection from Santa Barbara County may belong here: canyon of Mono Creek, 1,600 ft., upper Santa Ynez River watershed, *Chandler* 1460 (SBBG). The plants represented in this collection are immature, and the species is otherwise not known from Santa Barbara County.

37. Camissonia hardhamiae Raven, sp. nov. FIGURE 47

Herba annua robusta villosa pilis glandulosis brevioribus admixta, ad *C. intermedia* similis. Folia superiora lanceolata vel anguste ovata. Hypanthium 1.7–2 mm. longum, ostio 1.3–1.5 mm. diametro. Sepala 1.8–3.2 mm. longa, 0.8–1.2 mm. lata. Petala 2–4 mm. longa, 1.8–3.5 mm. lata, immaculata. Filamenta staminum episepalorum 1.5–2 mm.

longa, illa epipetalorum 1–1.5 mm. longa; antherae ca. 0.7 mm. longae. Pollinis granorum 70–80 per centum, 4– vel 5–porum. Stylus 3–4 mm. longus; stigma 0.7–1 mm. diametro, sub anthesi antheris circumnexum. Capsula 1.3–2.5 cm. longa, 1.3–1.6 mm. crassa surrecta vel in spiram unam contorta. Semina ca. 1.2 mm. longa, 0.6–0.7 mm. crassa. Chromosomatum numerus gameticus, $n=21$. Autogama.

TYPE: Calf Canyon, 3.7 miles northeast of Santa Margarita, San Luis Obispo County, California, 5 May 1963, *P. H. Raven* 18315 (DS 516765).

DISTRIBUTION (Figure 52): Very local, known only from a few localities in sandy soil in disturbed oak woodland, southernmost Monterey to central San Luis Obispo County, California; ca. 800–ca. 2,000 ft. alt.

SPECIMENS EXAMINED:

U.S.: CALIFORNIA: MONTEREY CO.: Sandy Valley, Big Sandy ca. 1.5 mi. NE. of intersection with Indian Valley Road, *Hardham* 10035A (DS). SAN LUIS OBISPO CO.: 4.5 mi. NE. of Santa Margarita, *Linsley & MacSwain* 59–87 (RSA), 59–88 (RSA), *Thorp* 62–33 (DS); 1.1 mi. N. of intersection with Parkhill Road on Calf Canyon Road, *Hardham* 2293 (LA); 1 mi. E. of Red Eagle Mine, 12 mi. S. of Shandon, *McMillan* 105 (CAS).

This local hexaploid species has almost certainly been derived from the diploid *C. micrantha* and the tetraploid *C. intermedia*, both of which grow in the area of *C. hardhamiae*. The hexaploid is quite similar to *C. micrantha*, but it can easily be distinguished by an examination of the pollen, *C. micrantha* having only an occasional 4-pored grain. *Camissonia hardhamiae* has broader leaves and thicker capsules than *C. micrantha* and is generally more robust. Its chromosome number has been determined in single plants from 3 populations, including the type collection (see Appendix). It has been found growing sympatrically with *C. micrantha* and *C. hirtella*.

Cammissonia hardhamiae is named in honor of Clare B. Hardham of Paso Robles, California, enthusiastic student of the flora of the area where it grows. Mrs. Hardham has contributed much to our knowledge of the flora of her area through her numerous collections.

38. Camissonia luciae Raven, sp. nov. FIGURE 49

Oenothera hirta var. *jonesii* sensu Munz, Bot. Gaz. 85: 262. 1928; pro parte.
Oenothera micrantha sensu Munz, N. Amer. Fl. II. 5: 160. 1965; pro parte.

Herba annua erecta robusta villosa eglandulosa, ad *C. micrantha* similis. Folia superiora lanceolata, 1.3–5.5 cm. longa, 1.2–2.5 cm. lata, basi rotundata vel truncata, apice acuminata, sessilia, sparse denticulata. Inflorescentia plerumque cinereo-pubescens. Hypanthium 2–3 mm. longum, ostio 1.5–1.8 mm. diametro. Sepala 2.5–4.5 mm. longa, 1–1.8 mm. lata. Petala 4–7 mm. longa, 2.2–5 mm. lata, saepe

mucronata, plerumque prope basin puncto rubro uno. Filamenta staminum episepalorum 1.2–6 mm. longa, illa epipetalorum 0.8–1.6 mm. lata; antherae 0.4–1 mm. longae. Pollinis granorum 25–60 percentum quadriporum. Stylus 3–6 mm. longus; stigma 1–1.2 mm. diametro, sub anthesi antheris staminorum longiorum vel rarissime et longiorum et breviorum circumnexum. Capsula ca. 1.5–2 cm. longa, 1.3–2 mm. crassa, transectione quadrangularis exsiccatis, subteretis in statu vivo non dessicata, in spiras 1.5–2+ contorta. Semina 1.3–1.5 mm. longa, 0.7–0.8 mm. crassa. Chromosomatum numerus gameticus, $n=21$. Autogama.

TYPE: Openings in *Adenostoma* chaparral, The Indians, 2,200 ft., Santa Lucia Mountains, Monterey County, California, 3 May 1963, *P. H. Raven* 18267 (DS 545885).

DISTRIBUTION (Figure 52): Locally common in openings in the chaparral, Santa Lucia Mountains, Monterey County, California, and scattered southward to San Benito, San Luis Obispo, and Santa Barbara Counties; 1,000–4,500 ft. alt.

SPECIMENS EXAMINED:

U.S.: CALIFORNIA: MONTEREY CO., SANTA LUCIA MTS.: Hastings Reservation, near Jamesburg, *Hoover* 2963 (POM, RSA, UC), 2964 (POM, RSA, UC), *Linsdale* 43 (CAS), 123 (COLO), in 1943 (CAS), *Cook & Cook* 842 (CAS, mix with *C. intermedia*), 680 (CAS); Conejo Creek 2 mi. below Jamesburg, *Bacigalupi* 1143 (DS, POM); road to Jamesburg 0.8 mi. from main road up Carmel Valley, R18226 (DS); The Indians, 2,200 ft., *Hardham* 5443a (CAS, RSA); trail to Ventana Double Cone between Pat Springs and Puerto Suelo, 4,000 ft., *Hardham* 10151 (DS, with *C. hirtella*); Tassajara Springs, *Kelley* in 1917 (CAS, with *C. intermedia*); Cachagua Creek, Santa Lucia Mts., *Howell* 30253 (CAS). SAN LUIS OBISPO CO.: Bill Hill Ranch at the foot of Caliente Mt., Caliente Range, 2,300 ft., *Twisselmann* 3489 (CAS); Crocker Grade, *Hardham* 12548 (DS). SANTA BARBARA CO.: "Santa Barbara," *Elmer* 3943 (DS, F, POM, RSA; probably from above Santa Barbara, in the mountains); upper Cuyama Valley, *Hoffmann* in 1929 (POM); Pine Corral Potrero near Salisbury Potrero, 4,500 ft., Sierra Madre Mts., *Muller & Blakley* 1014 (DS, SBBG); trail to Zaca Peak, *Eastwood* 616 (CAS); Miranda Pine Mt., 3,250 ft., *Graham* 545 (UC).

Camissonia luciae is a hexaploid species that parallels the widespread diploid *C. hirtella* in the variable notching of its petals. Presumably it has been derived from the diploid *C. hirtella* and the tetraploid *C. intermedia*, but it is rather easily separated from both by its relatively large flowers and pollen characteristics. The chromosome number of *C. luciae* has been determined in 7 individuals derived from as many populations, and including the type collection (see Appendix). It has been found growing sympatrically with *C. micrantha*, *C. hirtella*, and *C. intermedia*, especially often with the last-mentioned species.

295–655 O—68——10

39. Camissonia robusta Raven, sp. nov. FIGURE 41

Oenothera micrantha sensu Munz, N. Amer. Fl. II. 5: 160. 1965; pro parte.

Herba annua erecta robusta villosa, ad *C. micrantha* similis. Folia superiora latiora quam in *C. micrantha*, usque ad 12 cm. longa et 2 cm. lata. Inflorescentia semper pilis brevioribus glandulosis admixta. Hypanthium 1.8–3.7 mm. longa, ostio 1–2 mm. diametro. Sepala 2.6–4.2 mm. longa, 1.1–1.8 mm. lata. Petala 3.2–7 mm. longa, 2.5–6 mm. lata, plerumque prope basin puncto rubro uno vel punctis duabus. Filamenta staminum episepalorum 1.8–3 mm. longa, illa epipetalorum 1–1.5 mm. longa; antherae 0.8–1. 6 mm. longae. Pollinis granorum maximam partem 4-porum, rariore 5- vel 3-porum. Stylus 3–6.2 mm. longus; stigma 1–1.5 mm. diametro, sub anthesi antheris staminorum longiorum circumnexum. Capsula 1.4–2.5 cm. longa, 1.5–2 mm. crassa, transectione subquadrangularis in statu vivo, surrecta vel in spiram unam contorta. Semina 0.9–1.2 mm. longa, 0.6–6.7 mm. crassa. Chromosomatum numerus gameticus, $n=21$. Autogama.

TYPE: Disturbed soil along roadside, with *Orthocarpus purpurascens*, *Eschscholzia*, *Brassica*, near kilometer 201, 5.5 miles south of San Vicente, 950 ft., Baja California, 29 March 1962, *P. H. Raven* 17022 (DS 516799).

DISTRIBUTION (Figure 52): Coastal sage or chaparral, often in disturbed or open places, coastal San Diego County, California, and coastal northwestern Baja California, south to the vicinity of El Rosario at about 30° N. lat.; also on Santa Cruz, Santa Catalina, San Clemente, and Guadalupe Islands. From sea level to about 1,000 ft. alt. (to 3,500 ft. on Guadalupe Island).

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: LOS ANGELES CO. SANTA CATALINA I.: Avalon, *Trask* in 1896 (NY, UC, US). SAN CLEMENTE I.: Vicinity of Mosquito Harbor, *Abrams & Wiggins* 345 (DS, UC); N. coast, *Trask* 194 (NY, US); canyon S. of Lemon Tank, W. coast, *Munz* 6743 (POM). SAN DIEGO CO.: U.S. Hwy. 395, 2 mi. S. of turn to Lilac, R17458 (DS); 2 mi. E. of Pala, *Munz* 10364 (POM); 2 mi. E. of San Pasqual, R17408 (DS); Howard Canyon, La Jolla, *F. E. & E. S. Clements* 183 (COLO, F, GH, NY, PH, UC, UCSB); N. of Pt. Loma, *Stover* 149 (SD); bank of Dulzura Creek 3 mi. below Dulzura, *Wiggins* 2176 (CAS, DS, UC, WTU); Sweetwater R., base of San Miguel Mt., *Gander* 154.4 (POM, SD). SANTA BARBARA CO., SANTA CRUZ I.: Vicinity of Pelican Bay, *Abrams & Wiggins* 41 (F).

BAJA CALIFORNIA: Nachoguero Valley, *Schoenfeldt* 3409; Ensenada, *Bates* 2341 (DS); Todos Santos Bay, *Fish* in 1882 (F, UC); 6 mi. E. of El Rosario, *Wiggins* 17889 (DS); 6 mi. N. of Rancho Mesquital, *Wiggins* 16767 (DS). GUADALUPE I.: Near mouth of canyon at Northeast Anchorage, *Moran* 2891 (CAS, DS, GH, RSA); Northeast Anchorage, *Wiggins & Ernst* 222 (DS, UC), *Moran* 5661 (CAS, DS, RSA, SD, UC); near spring at top of island, N. end, ca. 1,200 m, *Lindsay* in 1948 (SD); Barracks Cove Cañon, *Copp* 151 (DS).

Camissonia robusta is one of the commoner species of its group throughout its mainland area, and the commonest species of the sec-

tion on Santa Catalina Island. On Santa Cruz Island this species is very rare. On San Clemente and Guadalupe Islands, the only other species of the section is the very different *C. quadalupensis*, but the two species are ecologically different and not known to grow together. The pollen of *C. robusta* is absolutely diagnostic, and its stout capsules, which are evidently quadrangular but not nearly so sharply so in living material as are those of *C. lewisii*, and erect, robust habit make this species distinctive in gross morphology also. It has been collected growing sympatrically with *Camissonia bistorta*, *C. lewisii*, *C. micrantha*, *C. hirtella*, and *C. intermedia*.

The chromosome number of *Camissonia robusta* has been determined in 29 individuals derived from 24 populations from localities scattered throughout the range of the species, including the type collection (see Appendix). This hexaploid is almost certainly derived from two species with which it occurs nearly throughout its rather limited range, the diploid *C. lewisii* and the tetraploid *C. intermedia*. It is morphologically intermediate between these two entities in all respects, although on the average somewhat more robust.

Moran (Madroño 11: 160. 1951; as *Oenothera micrantha*) has suggested that this species might be introduced on Guadalupe Island, where it was first collected in 1948. He bases his argument largely on the fact that this species was not discovered by any of a succession of collectors who visited the island and inevitably landed in the same region where *C. robusta* is now fairly common. This may be true, but judging from the phytogeographic relationships of Guadalupe Island and the scarcity of this species on San Clemente Island, I believe that it is equally likely that the species may simply have gone undetected and become more common recently. It will probably not be possible to resolve this question definitely.

Section VI. *Camissonia*

Camissonia sect. *Camissonia*

Oenothera sect. *Sphaerostigma* Seringe, *in* DC., Prod. 3: 46. 1828.

Oenothera subg. *Sphaerostigma* (Seringe) Torr. & Gray, Fl. N. Amer. 1: 508. 1840.

Camissonia sect. *Sphaerostigma* (Seringe) Raven, Brittonia 16: 284. 1964.

Annuals, the plants caulescent, with no well-defined basal rosette, but the leaves sometimes clustered near the base, plants not flowering from the base. Leaves narrow, subsessile. Inflorescence nodding at anthesis, becoming erect in fruit. Flowers opening near sunrise. Ovary lacking a sterile projection. Sepals reflexed singly or in pairs. Petals yellow, often with one to several red dots near the base, fading reddish, with no contrasting pattern visible in ultraviolet light. Stamens, style, and inside of hypanthium yellow, the stigma yellow or greenish yellow. Capsule regularly loculicidal, straight or somewhat flexuous,

subterete, more or less torulose, the seeds in one row in each locule, the friable central column much distorted by the seeds at maturity. Seeds with a scar at the micropylar end, blunt at the chalazal end, shining, dark brown, minutely lacunose, narrowly obovoid, more or less triangular in transection.

TYPE SPECIES: *Camissonia dentata* (Cav.) Reiche.

DISTRIBUTION: Brushy or open slopes and flats, southern Vancouver Island, British Columbia, southern Washington, southern Idaho, and western Wyoming south to western Colorado, central and northern Nevada, and throughout California to northernmost western Baja California (south to about 30°43′ N. lat.); said to have been collected once at Fort Huachuca, southern Arizona; also in western South America, mostly west of the Andes, from Arequipo (ca. 16° S. lat.), southern Peru to the vicinity of Lago Argentino and Santa Cruz (ca. 50° S. lat.), in Patagonia.

Camissonia sect. *Camissonia* is a close-knit group divided herein into 12 species with 4 additional subspecies. Two of these, *C. kernensis* and *C. campestris*, are self-incompatible diploids; two others, *C. pusilla* and *C. sierrae*, are self-compatible diploids; one is an autogamous hexaploid; and the remaining seven are autogamous tetraploids. One obviously closely interrelated group of species comprise the self-incompatible diploid *C. kernensis*, the autogamous diploid *C. pusilla*, and the two autogamous tetraploids *C. pubens* and *C. parvula*. These species differ from the others in their Great Basin habitat, and in having the sepals separating from one another when the flowers open. In the remaining species the sepals remain united in pairs. Relationships within this group are close, and the populations included here have generally been regarded as comprising only two species, the self-incompatible *C. campestris* (usually known, incorrectly, as *Oenothera dentata*) and the autogamous *C. contorta* (usually divided into *Oenothera contorta* var. *typica* and *O. contorta* var. *strigulosa*). The species that I have named *C. sierrae*, *C. benitensis*, and *C. integrifolia* have hitherto been too poorly represented in collections to attract attention; *C. lacustris* has been confused with *C. campestris* and *C. contorta* (sens. lat.); and the extremely closely related trio consisting of the tetraploid *C. strigulosa*, the hexaploid *C. contorta*, and the South American tetraploid *C. dentata* (some populations with $n=13$, the only instance of aneuploidy known in the genus) has in North America been regarded as comprising *Oenothera contorta* var. *strigulosa*, var. *epilobioides*, and var. *contorta*, the lines between these taxa not corresponding to those between the species recognized here. These might all conservatively be treated as *C. dentata* sens. lat., but I prefer to keep them separate for reasons that will be discussed in some detail below.

Camissonia kernensis subsp. *kernensis* was initially attributed to *Oenothera* subg. *Chylismia*, but I excluded it from that group in 1962 (Univ. Calif. Publ. Bot. 34: 115). On the other hand, *C. kernensis* subsp. *gilmanii* was first described as a variety of *C. campestris* ("*Oenothera dentata*"); I pointed out the conspecificity of the two taxa here grouped as *C. kernensis* to Dr. Munz in 1963, and he brought them together in 1965 (N. Amer. Fl. II. 5: 158–159). Part of what is here regarded as *C. kernensis* subsp. *gilmanii* was included by Munz (Bot. Gaz. 85: 259. 1928) in his concept of *Oenothera dentata* var. *johnstonii*, the type of which is *Camissonia campestris*. In the same 1928 treatment, Munz included all of the autogamous entities in this group in *Oenothera contorta*, with his var. *pubens* corresponding to *C. pubens*, his var. *flexuosa* to *C. pusilla* and *C. parvula*, his var. *typica* to much of *C. contorta*, and his var. *epilobioides* and var. *strigulosa* including the other autogamous taxa known to him.

Determinations of chromosome number, and in many cases pairing, have been made of 177 individuals from 166 populations of this section, including a few counts reported earlier by Lewis, Raven, Venkatesh, & Wedberg (Aliso 4: 73–86. 1958) and two reported by Gregory & Klein (Aliso 4: 505–521. 1960). The chromosome number for *Camissonia campestris* (as *Sphaerostigma dentatum* and var. *campestre*) was reported by Johansen (Proc. Nat. Acad. Sci. U.S. 15: 884. 1929; Amer. Journ. Bot. 16: 597. 1929), but without any indication of voucher specimens. As far as I know, these are all of the available reports for the section.

The degree of chromosomal structural heterozygosity in this section is low: of the 35 individuals of *Camissonia campestris* subsp. *campestris* examined, 3 had a ring of 4 chromosomes and 5 pairs and 1 had a chain of 3 plus a univalent and 5 pairs. Considering the two self-incompatible species in the section, *C. campestris* and *C. kernensis*, 49 individuals have been examined chromosomally, with the 4 just indicated being the only ones that were heterozygous—approximately 2 percent of the total. This is much lower than the more than 20 percent of 676 individuals of sect. *Chylismia* that were heterozygous for at least one reciprocal translocation, but significantly higher than in sect. *Holostigma*, where reciprocal translocations appear to play no role whatever in natural populations.

Several interploid natural hybrids, discussed in the following pages, shed light on the pattern of chromosomal evolution in sect. *Camissonia*. For example, in hybrids between the diploid ($n=7$) *C. campestris* subsp. *campestris* and the hexaploid ($n=21$) *C. contorta*, the maximum association of chromosomes observed was a chain of 8 chromosomes, a ring of 4, 2 chains of 4, 2 ring bivalents, and 2 rod bivalents. It is therefore obvious that the complete absence of multivalent configura-

tions in the hexaploid is genetically controlled, and does not reflect any great degree of differentiation between the three genomes present in this species. No multivalents have been found in any polyploid in this section, and it would appear that even if the two diploid genomes present in a tetraploid would, on the basis of their homology, pair completely, they are prevented from doing this genetically. Natural hybrids between the tetraploids *C. integrifolia* and *C. strigulosa*, with up to 10 bivalents, and artificial hybrids between the North American tetraploid *C. strigulosa* and the South American tetraploid *C. dentata*, which show few multivalent associations despite their high degree of sterility, tend to support this hypothesis (Raven & Moore, MS.).

In sect. *Camissonia*, therefore, it appears that diploid genomes may be brought together in any way that will produce highly fit combinations for particular ecological situations, and that these polyploids will soon (perhaps initially) be pair-forming and highly fertile regardless of the degree of chromosomal divergence between their diploid antecedents. There appears to be a wide gap between the group of species consisting of *C. kernensis*, *C. pusilla*, *C. pubens*, and *C. parvula*, and the other species of the section; none of the polyploids appears to bridge the gap between these two groups.

The synonymous name *Onothera torulosa* H. Lév., Monogr. Onoth. 176. 1905, requires special mention here; this name was an illegitimate substitute for most of the species in this section published earlier, and it is not practical to cite it in the synonymy of all of these names or to attempt to typify it by one of these concepts; as far as I know, the concept has never been taken up by any author other than Léveillé.

40. Camissonia kernensis (Munz) Raven, Brittonia 16: 284. 1964.

Robust, erect annual, often well branched, from a prominent or poorly developed basal rosette, the plants 5–30 cm. tall, densely villous or glandular pubescent to subglabrous. Leaves very narrowly to narrowly elliptic, more rarely lanceolate, 1–3.8 (–5.5) cm. long, 0.2–0.5 cm. wide, sparsely serrate, the apex acuminate, the base narrowly cuneate, much reduced and bract-like in the inflorescence. Inflorescence usually densely glandular-pubescent, sometimes with an admixture of longer trichomes. Hypanthium 2.2–3.8 (–5) mm. long, 1.8–2.8 (–4) mm. across at the summit, villous within, with a red dot within at the base of each anther. Sepals 5–9 (–11) mm. long, 1.3–2 mm. wide, reflexed separately. Petals 8–15 (–18) mm. long, 5.5–12 (–16) mm. wide, with two large red dots at the base of each one. Filaments of the episepalous stamens 3.5–5.5 (–7) mm. long, those of the epipetalous ones 1.3–2 (–4.5) mm. long; anthers 1.8–2 (–3) mm. long. Style 7–10 (–14) mm. long, villous near the base; stigma 1–2 (–2.5) mm. in diameter, held well above the anthers at anthesis. Capsule 2.2–3.7 cm. long, 1.5–1.7 mm. thick, subsessile or

on a pedicel up to 15 mm. long. Seeds 1.1–1.2 mm. long, 0.5–0.6 mm. thick. Gametic chromosome number, $n = 7$. Self-incompatible.

DISTRIBUTION (Figure 46): Desert washes and in canyons, northeastern Kern County to near Victorville and the Providence Mountains in San Bernardino County, southern Inyo County, and near Benton Station, southern Mono County, California; also in western Clark and Nye Counties, Nevada; 2,500–6,000 ft. alt.

Although most populations of the two subspecies comprising this species are easily assignable to one or the other, a number of others are intermediate and assignable only with great difficulty. Collectively, the species is sharply distinct from all others in its flower size, pubescence, and sepal characteristics.

40a. Camissonia kernensis subsp. **kernensis**

Oenothera kernensis Munz, Amer. Journ. Bot. 18: 737. 1931.
Oenothera kernensis subsp. *kernensis*; Munz, N. Amer. Fl. II, 5: 159. 1965.

Plants compact, 5–15 (–22) cm. tall, covered everywhere with long, white trichomes, the leaves clustered at the base. Capsule on a prominent pedicel 3–15 mm. long. Gametic chromosome number, $n = 7$. Self-incompatible.

TYPE: Sandy slopes and openings, east slope of Walker Pass, Freeman Canyon, 4,500 ft., Kern County, California, 13 May 1930, *F. W. Peirson* 8822 (POM; isotype, K).

DISTRIBUTION (Figure 46): Sandy slopes and flats, often with *Artemisia tridentata* and *Yucca brevifolia*, northeastern Kern County, California, from El Paso Peaks to the vicinity of Claraville and near Lake Isabella, north to Grapevine Canyon; 2,800–5,700 ft. alt. Often locally abundant.

Vouchers for chromosome number (4 individuals, 3 populations), $n = 7$:

U.S.: CALIFORNIA: KERN CO.: Walker Pass, W. slope, 5,000 ft., *Munz* 22581 (DS, RSA): 2.8 mi. W. of summit of Walker Pass, R12811; Freeman Canyon 3.4 mi. E. of summit of Walker Pass, R12763 (2 plants: ARIZ, DS, GH, SD, UC, US, WTU).

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: KERN CO.: Grapevine Canyon, 2,800 ft., *Twisselmann* 7117 (CAS, mixture with *C. campestris*); upper end of Short Canyon, *Linsley & MacSwain* 60–18 (RSA, UC); head of Indian Wells Canyon, 5,700 ft., *Twisselmann* 4525 (CAS, DS); NE. flank of Morris Peak, 4,175 ft., *Twisselmann* 7140 (CAS, DS, SBBG); Horse Canyon, Scodie (Kiavah) Mt., 5,300 ft., *Twisselmann* 8178 (CAS, DS, RSA); Weldon, 2,400 ft, R17559 (DS); 9.7 mi. S. of Weldon, 3,100 ft., R17563 (DS); 5 mi. NW. of Dove Well, *Rude* 408 (DS); divide between Kelso Canyon and Kelso Valley, 4,650 ft., *Twisselmann* 6912 (CAS, DS); Piute Mts., Harris Grade above Kelso Canyon, 3.1 mi. W. of Shorty's Place, 5,420 ft., *Twisselmann* 2799 (CAS); Erskine Creek, 4–5,000 ft., *Purpus* 5083 (UC, mixture with *C. hirtella*); Iron Canyon, El Paso Mts., ca. 3,300 ft., *Budgett* 30 (CAS); Dove Spring Canyon 25 mi. SW. of Inyokern, *Budgett* 54 (CAS).

First described as a member of *Oenothera* subg. *Chylismia* because of its stalked capsule, *Camissonia kernensis* subsp. *kernensis* is in the overwhelming majority of its characteristics obviously a member of sect. *Camissonia*. At the margins of its rather restricted range, it intergrades completely with *C. kernensis* subsp. *gilmanii* (*Oenothera dentata* var. *gilmanii*), an undoubted member of this group. Ten plants from the locality of R17559, cited above, were tested for self-incompatibility by caging the plants in the field and selfing and outcrossing them, with subsequent examination of pollen-tube growth. All were found to be self-incompatible. *Camissonia kernensis* subsp. *kernensis* is, at the head of Short Canyon, the principal pollen source of the large oligolectic bee *Andrena* (*Onagrandrena*) *mojavensis* Linsley & MacSwain, not known from any other locality (Linsley, MacSwain, & Raven, Univ. Calif. Publ. Entom. 33: 59–98. 1964). Other oligolectic species of *Onagrandrena* likewise visit the plant here and on Walker Pass and are undoubtedly important in the outcrossing of these self-incompatible individuals. The flowers of *Camissonia kernensis* subsp. *kernensis* open before sunrise, and considerably before those of *C. campestris* at most of its localities (Linsley et al., op. cit.).

Camissonia kernensis subsp. *kernensis* grows sympatrically with *C. campestris*, which like it is self-incompatible at a number of localities; no hybrids have been observed, even when, as at Short Canyon, Kern County, California, the plants grow intermixed and are known to be visited by the same species of bees. *Camissonia kernensis* subsp. *kernensis* likewise grows sympatrically with *C. pubens*, *C. strigulosa*, *C. integrifolia*, and *C. contorta*.

40b. Camissonia kernensis subsp. **gilmanii** (Munz) Raven, comb. nov.

Oenothera dentata var. *johnstonii* sensu Munz, Bot. Gaz. 28: 259. 1928; pro parte.

Oenothera dentata var. *gilmanii* Munz, Leafl. West. Bot. 2: 87. 1938. *Oenothera kernensis* subsp. *gilmanii* (Munz) Munz, N. Amer. Fl. II. 5: 159. 1965.

Oenothera kernensis subsp. *mojavensis* Munz, N. Amer. Fl. II. 5: 159. 1965. Type: 3 mi. W. of Pilot Knob, 900 m, western San Bernardino Co., Calif., 20 March 1947, *P. A. Munz* 11666 (RSA 38224; isotypes, ARIZ, CAS, COLO, SD, WTU).

Plants less compact, to 30 cm. tall, covered everywhere with short glandular pubescence, usually with a few scattered longer trichomes, or subglabrous, with few glandular trichomes, the leaves not markedly clustered at the base. Capsule subsessile or on a pedicel to 5 mm. (rarely to 15 mm.) long. Gametic chromosome number, $n=7$. Self-incompatible.

Type: Bradbury Wash, 3,000 ft., Inyo County, California, 6 June 1937, *M. F. Gilman* 2587 (POM).

Distribution (Figure 46): Desert washes and slopes, from the vicinity of Red Rock Canyon, Kern County and Victorville and the

Providence Mountains, San Bernardino County, California, north to westernmost Clark and Nye Counties, Nevada, and the southern half of Inyo County, California; also collected once near Benton Station, southern Mono County, California. From 2,500–6,000 ft. alt.

Vouchers for chromosome number (5 individuals, 5 populations), $n=7$:

U.S.: CALIFORNIA: INYO CO.: Trona to Death Valley Road, N. base of Panamint Mts., edge of Panamint Valley, *Lewis & Mosquin* 1119; 5.4 mi. from Emigrant Junction on road to Wildrose Station, *Lewis & Mosquin* 1123. SAN BERNARDINO CO.: Dawes Siding, between Cima and Kelso, R11926; road to Camp Irwin 26.6 mi. N. of U.S. Hwy. 466 at Barstow, R11944. NEVADA: NYE CO.: Wash below Cane Springs, R18947.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: INYO CO.: 10 mi. N. of Shoshone on road to Bradbury Well, ca. 3,000 ft., *Hitchcock* 6106 (DS NY, POM, RM, RSA, US, WS, WTU); Great Falls Canyon, Argus Mts., *Wheeler & Richardson* in 1930 (CAS, F, LA, LAM, UC, US); Mill Creek Canyon, Panamint Mts., 1,300–1,700 m, *Coville & Funston* 759 (C, DS, GH, PH, US); Epsom Salt Works, Hidden Spring region S. of Wingate Wash, 2,000 ft., *Train* 568 (ARIZ, COLO, DS, OSC, US); Cave Springs, *Jaeger* in 1927 (POM); Lee District (N. of Darwin), at Grape Vine Spring, *Austin* 539 (UC); 6 mi. NE. of Pilot Knob, Meerchaum Spring, *Miller* in 1920 (CAS). KERN CO.: U.S. Hwy. 395, 5 mi. N. of Johannesburg, 3,150 ft., *Campbell* 13406 (RSA); Red Rock Canyon, 2,800 ft., *Benson* 3411 (POM); Haiwee, *Davidson* 2820 (LAM); E. fork of Last Chance Canyon, El Paso Mts., 3,000 ft., *Peñalosa* 473A (CAS). MONO CO.: Benton Station, 5,500 ft., *Robinson & Linder* in 1935 (Fresno State College herb.). SAN BERNARDINO CO.: County road from Wheaton Springs to Nipton road S., ca. 11 mi. N. of Cima, *Ferris & Bacigalupi* 13293 (ARIZ, DS, RM, US, WS, WTU); 10 mi. SW. of Garlic Spring, *Munz & Keck* 7869 (GH, POM); 2 mi. N. of third summit out of Barstow, 8 mi. SW. of Bicycle Lake, 2,800 ft., *Wolf* 6532 (ARIZ, DS, LA, NY, RM, RSA, UT, WS); 5 mi. E. of Cima, *Munz* 13947 (DS, POM, UC); 5 mi. W. of Columbia Mine, Providence Mts., 1 mi. E. of Union Pacific R.R., 3,300 ft., *Wolf* 10649 (DS, RSA, WTU); 8 mi. E. of Victorville, *Jaeger* in 1932 (POM). NEVADA: CLARK CO.: Nipton, 3,000 ft., *Jones* in 1907 (POM); 5 mi. below Deer Creek, 6,000 ft., Charleston Mts., *Raedar* 181 (COLO); Frenchman Flat 11 mi. N. of Mercury, R18854 (DS). NYE CO.: W. of Cane Springs, ca. 4,000 ft., *Rickard & Beatley* in 1959 (RSA, UC); W. Yucca Flat Drainage Basin, 4,800 ft., *Beatley* 2924 (DS, RSA).

Plants of *Camissonia kernensis* subsp. *gilmanii* in the vicinity of Cima, San Bernardino County, California, approach those of subsp. *kernensis* in their relatively low stature and unusually abundant eglandular pubescence. Closer to the restricted range of subsp. *kernensis*, the two subspecies intergrade completely. In general, plants from the southern part of the range of subsp. *gilmanii* are relatively lower and less glandular, and often with more obviously crisped leaves, than those from farther north; it was on this basis that Munz described a third subspecies, *Oenothera kernensis* subsp. *mojavensis*. Study of more abundant herbarium material has convinced me that these trends do not need to be reflected in the formal taxonomy of the

group, especially since the geographical separation of the two sorts of plants is not complete.

Camissonia kernensis subsp. *gilmanii* has been found growing sympatrically with *C. campestris* at several localities without any evidence of hybridization, even though both entities consist entirely of self-incompatible individuals and are generally visited by the same bee species. Thus, 3 miles west of Pilot Knob, San Bernardino County, California, at an elevation of ca. 3,400 ft., P. A. Munz collected these two entities growing together; here *C. kernensis* subsp. *gilmanii* was restricted to the higher ground, and often grew in coarse gravelly soil, whereas *C. campestris* grew in the loose sandy soil of a wash. A mixed collection from Red Rock Canyon, Kern County, California (*Brown* in 1946, LA) suggests that the two species grow sympatrically at this locality also. Similar ecological relationships were observed near the head of Short Canyon, Kern County, California, where *C. campestris* grows in the sandy soil of the wash bottom, while *C. kernensis* subsp. *kernensis* is largely restricted to more stable slopes at the head of the wash.

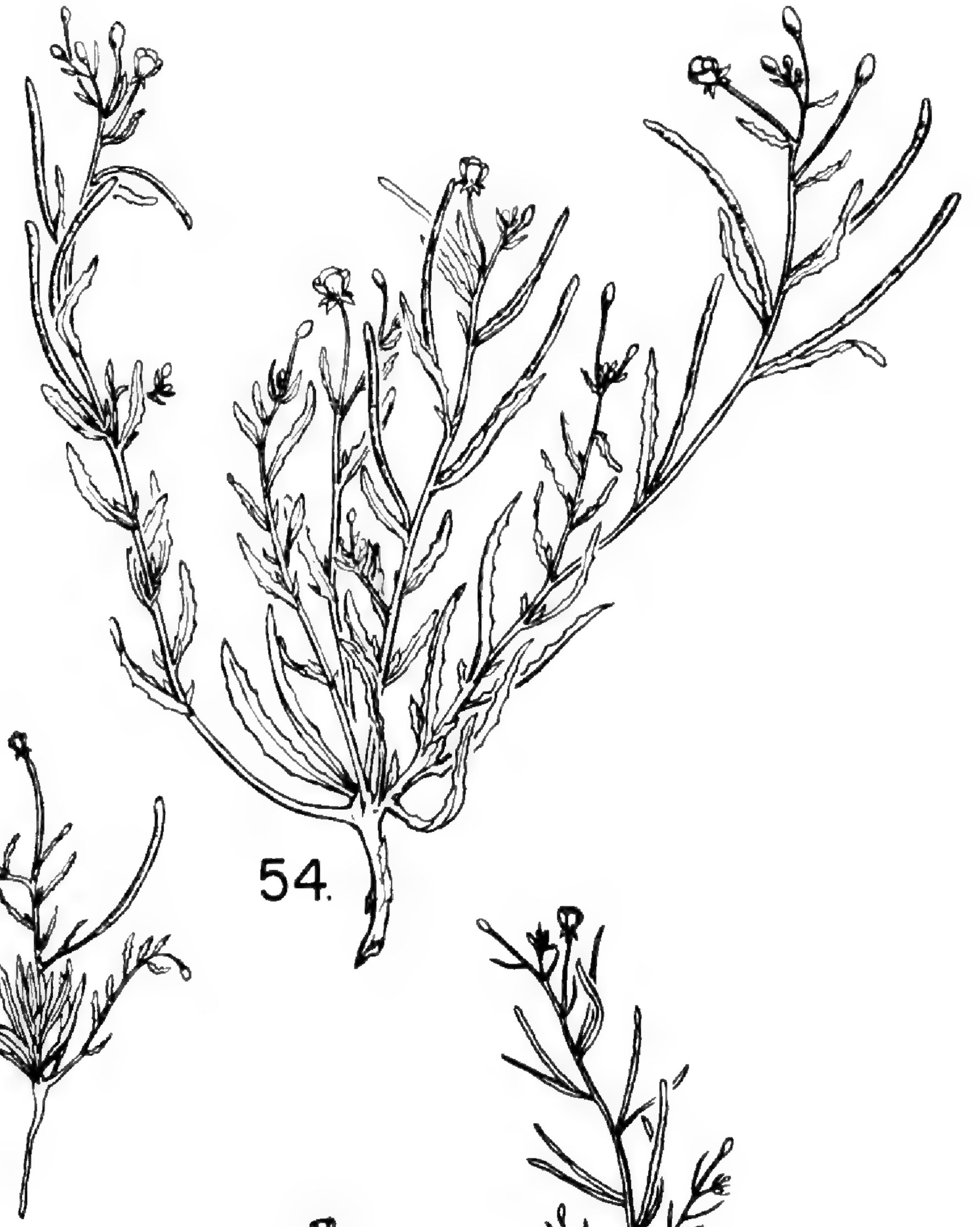
The self-incompatibility of *Camissonia kernensis* subsp. *gilmanii* was determined by pollen-tube growth following self- and cross-pollination in six individuals of R18947 from Nye County, Nevada, cited above.

41. Camissonia pusilla Raven, sp. nov. FIGURE 53

Oenothera contorta var. *flexuosa* sensu Munz, Bot. Gaz. 85: 253. 1928; and N. Amer. Fl. II. 5: 156. 1965; pro parte.

Herba annua tenuis 2–22 cm. alta, plerumque e basi ramis plurimis rosulaque bene evoluta. Plantae glanduloso-pubescentes, praecipue in inflorescentibus, et plerumque pilis longioribus eglandulosis admixtae, prope basin plantarum densiore. Folia linearia, 1–3 cm. longa, 0.4–1.8 mm. lata, plerumque purpureo-maculata, serrulata. Hypanthium 0.8–1.6 mm. longum, ostio 0.7–1.1 mm. diametro, intus glabrum. Sepala 1.2–2 mm. longa, 0.3–0.8 mm. lata, unumquidque sub anthesi discedens, alabastro apices sepalorum discreti. Petala 1.8–3.1 mm. longa, 0.8–1.5 mm. lata, rare prope basin punctibus duabus rubris maculata. Filamenta staminorum episepalorum 0.8–2 mm. longa, illa epipetalorum 0.4–0.9 mm. long; antherae 0.3–0.4 mm. longae. Stylus 1.6–3.2 mm. longus, glaber; stigma 0.5–1 mm. diametro sub anthesi antheris circumnexum. Capsula 1.8–3.2 cm. longa, 0.6–0.9 mm. crassa, subsessilis vel pedicelo usque ad 2 mm. longo, non rostrata. Semina 0.7–0.8 mm. longa, ca. 0.4 mm. crassa. Chromosomatum numerus gameticus, $n=7$. Autogama.

TYPE: On sagebrush (*Artemisia tridentata*) covered slopes 2.5 miles west of U.S. Hwy. 395 on U.S. Hwy. 50, 5,100 ft., Washoe County, Nevada, 28 May 1962, *P. H. Raven* 17867 (DS).



FIGURES 53–55.—Species of *Camissonia* sect. *Camissonia*, × ¾: 53, *C. pusilla* (*Raven* 17463, DS); 54, *C. pubens* (*Twisselmann* 7048, DS); 55, *C. parvula* (*Raven* 17864, DS).

Distribution (Figure 56): Scattered in sandy soil on open or brushy slopes, Franklin and Grant Counties, southeastern Washington, and Elmore and Payette Counties, west-central Idaho, south through the Great Basin to southern Inyo and the Providence Mountains of northeastern San Bernardino County, California; southern Nye County, Nevada; and Washington County, southwestern Utah;

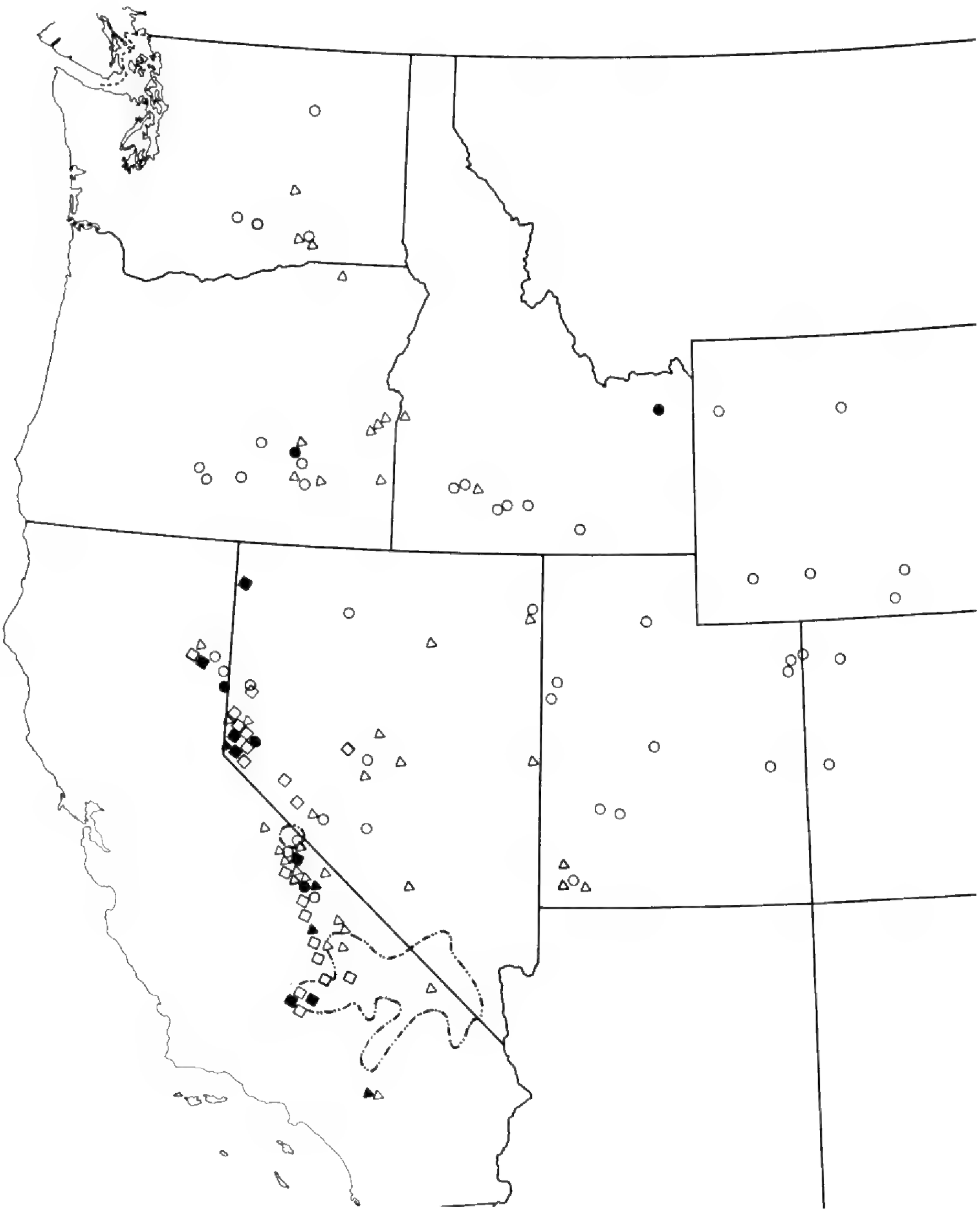


Figure 56.—Western United States, showing ranges of mainly autogamous species of *Camissonia* sect. *Camissonia*, the range of the related larger flowered, self-incompatible *C. kernensis* outlined by dotted line: △=*C. pusilla*, with ▲=diploid chromosome counts ($n=7$); ◇=*C. pubens*, with ◆=tetraploid counts ($n=14$); ○=*C. parvula*, with ●=tetraploid counts ($n=14$).

local in the eastern San Bernardino Mountains, San Bernardino County, California. From ca. 400–9,500 ft. alt.

Vouchers for chromosome number (5 individuals, 5 populations), $n=7$:

U.S.: California: inyo co.: Carroll Creek ca. 1 mi. above Mt. Whitney Pack Station, 5,900 ft., E. slope of the Sierra Nevada, R17541; ca. 4 mi. S. of Oasis, *Klein* 354 (RSA); near Black Ace Mine, just W. of summit of Westgard Pass, White Mts., *Lewis* 1091 (LA, RSA). san bernardino co.: Cactus Flat, San Bernardino Mts., 5,900 ft., R17463. Nevada: washoe co.: 2.5 mi. W. of U.S. Hwy. 395 on U.S. Hwy. 50, 5,100 ft., R17867 (type collection).

Representative specimens examined:

U.S.: California: inyo co.: 4 mi. W. of Lone Pine, 4,700 ft., *Alexander & Kellogg* 2786 (mixture with *C. parvula*); Lake Sabrina road, 8,500 ft., *Benson* 6020 (POM); Bishop Creek, 5,000 ft., *Hall & Chandler* 7244 (POM, UC); 0.5 mi. W. of Willow Spring, Last Chance Mts., 5,800 ft., *Roos* 6363 (CAS, DS, RSA, UC); Jackass Spring, Hunter Mt., Inyo Mts., 6,600 ft., *DeDecker* 1400 (RSA); Alabama Hills, 4,800 ft., *Howell* 33226; Lone Pine, 7,000 ft., *Jones* in 1897 (GH, NY, POM, US); Argus Mts., 5,800 ft., *Hall & Chandler* 7089 (UC); Wonoga Peak, 9,000–9,500 ft., *Howell* 25419 (CAS, RSA; with *C. pubens*); Mill Creek Canyon, Panamint Mts., 1,300–1,700 ft., *Coville & Funston* 762 (DS, NY, US); near Crystal Spring, Coso Mts., 1,850 m., *Coville & Funston* 938 (DS, NY, US). lassen co.: 2 mi. N. of Susanville, *Gillespie* 9346 (DS). mono co.: Rock Creek, 6,700 ft., *Munz* 11785 (NY, RSA); near Benton, *Robinson & Linder* c26 (COLO, RSA, WTU), *Eastwood & Howell* 9547 (CAS, mixture with *C. parvula;* RSA); 5 mi. N. of Sherwin Grade, 1,750 m., *Munz* 11075 (C, GH, POM, UC, US); S. of Mono Lake, 4 mi. N. of Mono Mills, *Keck* 2882 (DS). san bernardino co.: 1 mi. SE. of Tecopa Pass, Kingston Range, *Alexander & Kellogg* 2365 (POM, UC); Cactus Flat, San Bernardino Mts., 6,000 ft., *Munz* 10519 (POM), *Jones* in 1926 (CAS, POM). Idaho: elmore co.: Glen's Ferry, *Davis* 85–36 (IDS). payette co.: Willow Creek E. of Payette, *Christ* 9447 (NY) Nevada: elko co.: Cobre, 6,000 ft., *Jones* in 1906 (POM); Elko to Wendover road, *Hutchings* in 1932 (UT); Toana Range, 5 mi. E. of Shafter, *Maguire* 16892 (NY, mixture with *C. parvula*). esmeralda co.: Candelaria, *Shockley* 247 (NY, mixture with *C. parvula*). eureka co.: U.S. Hwy. 40, 2.9 mi. W. of Carlin, R18534 (DS). lander co.: 3 mi. N. of Birch Creek, *J. M. & M. A. R. Linsdale* 780A (CAS). nye co.: Near Potts Ranch, near Potts, *Goodner & Henning* 330 (POM); 4 mi. S. of Millett, *J. M. & M. A. R. Linsdale* 694 (CAS); S. end of Rainier Mesa, 7,500 ft., *Beatley & Carl* 2616 (herb. Nevada Test Site, Mercury, Nev.). washoe co.: 2 mi. SW. of Steamboat Springs, *Canby* 181 (POM); Truckee Pass, 4,500 ft., *Kennedy* 1306 (DS, RM, UC, US). white pine co.: 2 mi. SW. of Baker, *Maguire* 20849 (UT). Oregon: Blue Mts., *Cusick* in 1897 (GH); eastern Oregon, *Howell* in 1880 (US). harney co.: Ca. 26 mi. S. of Folly Farm and near Manns Lake, *Hitchcock & Muhlick* 21131 (DS, RM, WS, WTU); 8 mi. W. of Riley, *Peck* 13840 (DS, F); Squaw Butte, *Gilkey* (OSC); 4.7 mi S. of Narrows, R18444 (DS). malheur co.: 4 mi. W. of Vale, *Peck* 20641 (UC); near Harper Ranch, 900 m., *Leiberg* 2221 (DS, F, GH, NY, POM, UC, US); ca. 15 mi. SW. of Vale, *Hitchcock* 20636 (WTU); Rome, *Peck* 21789 (UC). Utah: iron co.: NE. of Enterprise, 5,500 ft., *Hall* EN16 (F, UT). washington co.: Anderson's Ranch, *Maguire & Blood* 1459 (POM, RM, UC); mountain meadows 50 mi. NW. of St. George, 1877, *Palmer* 166 (GH, NY). Washington: franklin co.: Pasco, *Piper* 2965 (GH). grant co.: Junction of Crab and Douglas Creeks, 2,000–3,000 ft., *Sandberg & Leiberg* 263 (C, CAS, DS, F, GH, NMC, NY, RM, UC, US, WS, WTU).

This diploid species is closely similar to the tetraploids *C. parvula* and *C. pubens*, differing from the former in its long, spreading trichomes and well-developed basal rosette and from the latter in its more slender habit, narrower leaves, and smaller flowers and seeds. At its type locality and elsewhere, *C. pusilla* grows sympatrically with *C. pubens*, and, as indicated above, it often grows sympatrically with *C. parvula;* at all such localities the entities are sharply distinct. On the other hand, northern populations of *C. pusilla* are occasionally somewhat difficult to distinguish from those of *C. parvula*, commoner northward, when the plants are relatively glabrous and depauperate, and chromosome counts from the northern localities of *C. pusilla* would be most helpful.

A collection said to be from Kramer, San Bernardino County, California, *K. Brandegee* in 1913 (UC), consists of a mixture of this species with *C. parvula;* the locality is very probably in error (cf. Raven, Univ. Calif. Publ. Bot. 34: 110. 1962).

Camissonia pusilla includes much of the material referred by Munz (Bot. Gaz. 85: 253–254. 1928; and subsequently) to *Oenothera contorta* var. *flexuosa*, that entity consisting of a mixture of this species, the tetraploid *C. parvula*, and misidentified specimens of the very different hexaploid *C. contorta*. In 1964 (Brittonia 16: 284. 1964), I considered *C. pusilla*, *C. parvula*, and *C. pubens* to be best regarded as comprising a single taxonomic species, *C. parvula;* I also annotated a number of specimens during the period when I held this view. On the other hand, Munz (N. Amer. Fl. II. 5: 156. 1965) recognized *C. pubens* as a distinct species, but unaccountably retained *C. parvula* and *C. pusilla* as *Oenothera contorta* var. *flexuosa* as he had done in 1928. As mentioned above, *C. contorta* is a very distinct hexaploid, in which the sepals are reflexed in pairs; however, depauperate individuals can sometimes be confused with those of *C. parvula*.

42. Camissonia pubens (S. Wats.) Raven, comb. nov. FIGURE 54

Chamissonia contorta var. *pubens* (S. Wats.) Kearney, Trans. N.Y. Acad. Sci. 14: 37. 1894.

Sphaerostigma contortum var. *pubens* (S. Wats.) Small, Bull. Torrey Cl. 23: 189. 1896.

Sphaerostigma pubens (S. Wats.) Rydb., Bull. Torrey Cl. 33: 146. 7 April 1906.

Sphaerostigma orthocarpum A. Nels. & Kennedy, Proc. Biol. Soc. Wash. 19: 155. 12 November 1906. Type: Pyramid Lake, Washoe Co., Nevada, 19 May 1905, *P. B. Kennedy* 1015a (RM).

Oenothera pubens (S. Wats.) Munz, N. Amer. Fl. II. 5: 156. 1965.

Similar to *C. pusilla*, but differing in the more robust habit, the stouter stems to 38 cm. long. Leaves narrowly lanceolate, 1.5–4.5 cm. long, 0.2–0.6 cm. wide, undulate-serrate, acuminate at the apex, narrowly cuneate at the base. Hypanthium 1.3–3 mm. long, 0.8–2 mm. wide at the summit, usually pubescent in lower half within, often with a small red dot at the base of each filament. Sepals 2.2–3.8 mm.

long, 0.8–1.3 mm. wide. Petals (2.2–) 3–4 mm. long, (1.3–) 1.8–3 mm. wide, often with one to several red dots near the base. Style 3.2–4.1 mm. long; stigma 1.2–1.4 mm. in diameter. Capsule (1.8–) 2.6–5 cm. long, 0.8–1.2 mm. thick. Seeds 1–1.1 mm. long, ca. 0.4 mm. thick. Gametic chromosome number, $n=14$.

TYPE: Carson City, Ormsby County, Nevada, May 1868, *S. Watson* (GH; isotype, US).

DISTRIBUTION (Figure 56): Sandy, often sagebrush-covered slopes and flats from Lassen County, California, and northern Washoe County, Nevada, south to southwestern Lander and central Mineral Counties, Nevada, and southern Inyo and northeastern Kern Counties, California; 3,000–9,500 ft. alt.

Vouchers for chromosome number (9 individuals, 9 populations), $n=14$:

U.S.: CALIFORNIA: KERN CO.: Weldon, R17537; 3.4 mi. E. of summit of Walker Pass, R12764. LASSEN CO.: 4.8 mi. N. of Milford, R17873. MONO CO.: 2.2 mi. S. of N. turn to Sherwin Grade, R14294. NEVADA: ORMSBY CO.: U.S. Hwy. 50, 2 1 mi. W. of junction with U.S. Hwy. 395, R17862; 2 mi. S. of Carson City R18406. WASHOE CO.: 7.5 mi. S. of Vya, ca. 6,500 ft. R17883; 4.7 mi. W. of U.S. Hwy. 395 on road to Mt. Rose, 5,200 ft., R18410; 2.5 mi. W. of U.S. Hwy. 395 on U.S. Hwy. 50, 5,100 ft., R17866.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: INYO CO.: Wonoga Peak, 9,000–9,500 ft., *Howell* 25420 (CAS, RSA, US); near end of Mt. Whitney road, *Kerr* in 1937 (CAS); Carroll Creek, 5,500 ft., *Howell* 33378 (CAS); Olancha, *Hoffmann* in 1929 (CAS); Bishop Creek, 6,700 ft., *Howell* 33520 (CAS); 5 mi. W. of summit of Mountain Spring Canyon, *Hoffmann* in 1929 (POM); Onion Valley road, *Howell* 33430 (CAS); Sage Flat to Olancha Pass, ca. 7,000 ft., *Howell* 26701 (CAS); Taboose Creek, 6,500 ft., R9702 (CAS); Nine-mile Canyon, 5,000 ft., *Ripley & Barneby* 5867a (CAS); Snake Hill, 5 mi. W. of Independence, 5,000 ft., *Kerr* in 1937 (CAS). KERN CO.: 19 mi. above Weldon on road to Walker Pass, 4,500 ft., *Munz* 13357 (RSA, mixture with *C. strigulosa;* WTU); 1.9 mi. E. of summit of Walker Pass, R12814 (DS); W. slope of Walker Pass, near summit, *Twisselmann* 7048 (CAS, DS); Piute Mt. to Walker Basin road, 5,950 ft., *Twisselmann* 3650 (CAS); Weldon, R18790 (DS); Horn Brothers Sawmill 3.6 mi. W. of Claraville, Piute Mts., 6,200 ft., *Breedlove* 4008 (DS); Erskin Creek, 4,000–5,000 ft., *Purpus* 5365 (UC). LASSEN CO.: Honey Lake, *Brandegee* in 1892 (UC); between Susanville and Leavitt Lake, *Gillespie* 9351a (DS); vicinity of Doyle Station, 1,290 m, *Eggleston* 6741 (GH, NY, US). MONO CO.: Sonora Junction, 7,200 ft., *Ripley & Barneby* 5804 (CAS, NY). NEVADA: DOUGLAS CO.: Clear Creek, 10 mi. SW. of Carson City, *Archer* 6055 (POM). LANDER CO.: Along roadside to Buzanes, ca. 25 mi. N. of Ione, *Goodner & Henning* 690 (DS, NY, POM). MINERAL CO.: E. slopes of Wassuk Range, near Big Indian Mt., 9,500 ft., *Archer* 7153 (ARIZ, POM); Hawthorne, *Jones* in 1882 (POM); 6–7 mi. from mouth, up Cory Creek, Wassuk Range, 7,400 ft., *Archer* 6951 (POM). ORMSBY CO.: Empire City, *Jones* 3870 (CAS, F, PH, UC); Carson City, 1,446 m, *Baker* 971 (CAS, F, GH, NMC, NY, POM, RM, UC, US). STOREY CO.: Virginia City, *Jones* in 1882 (POM); 1.8 mi. SE. of Five Mile House, 6,800 ft., *Adams* 31 (UC). WASHOE CO.: 5 mi. N. of Poeville, NW. of Reno, 5,000 ft., *Tillotson* 99 (RSA, UC); Reno, *Jones* in 1903 (POM);

Verdi, *Sonne* in 1889 (F); Lakeview, between Carson City and Franktown, *K. Brandegee* in 1913 (UC).

This distinctive tetraploid species occurs sympatrically with *C. pusilla*. It has also been found growing together with *C. parvula*, *C. kernensis* subsp. *kernensis*, *C. strigulosa*, *C. integrifolia*, and *C. contorta*, with no evidence of interspecific hybridization. The tetraploid chromosome voucher from northern Washoe County, Nevada, is rather doubtfully referred here, and more information is needed about the populations in the northern portion of the range of this species. This entity has generally been regarded as distinct and has rarely been confused with any other species since it was first described in 1873, as can readily be seen from the synonymy.

43. Camissonia parvula (Nutt. ex Torr. & Gray) Raven, Brittonia 16: 284. 1964. FIGURE 55

Oenothera parvula Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 511. 1840.
Sphaerostigma parvulum (Nutt. ex Torr. & Gray) Walp., Rep. 2: 78. 1843.
Sphaerostigma contortum var. *flexuosum* A. Nels., Bot. Gaz. 40: 58. 1905. Type: Point of Rocks, Sweetwater Co., Wyo., 16 June 1898, *A. Nelson* 4760 (RM; isotypes, GH, US).
Sphaerostigma filiforme A. Nels., Bot. Gaz. 40: 57. 1905. Type: New River (Reese's River), Utah, 28 May 1889, collector not known (MO).
Sphaerostigma flexuosum (A. Nels.) Rydb., Fl. Rocky Mts. 601. 1917.
Oenothera contorta var. *flexuosa* (A. Nels.) Munz, Bot. Gaz. 85: 253. 1928.

Slender annuals closely similar to *C. pusilla*, but differing as follows: basal rosette absent, with one or more wiry, naked stems arising from the base; pubescence strigulose, dense or wanting, or very rarely spreading, the plants usually with a sparse admixture of glandular trichomes, especially in the inflorescence, but often subglabrous; flowers sometimes larger, the hypanthium up to 2 mm. long; sepals to 2.2 mm. long and 1.1 mm. wide; petals to 3.6 mm. long.

TYPE: Probably from southern Idaho ("toward Lewis' River"), July or August 1834, *T. Nuttall* (NY; isotype, BM).

DISTRIBUTION (Figure 56): Sandy slopes, often under sagebrush, from Okanagan and Yakima Counties, Washington; Elmore and Fremont Counties, Idaho; and Teton, Washakie, and Carbon Counties, Wyoming, south through westernmost Colorado (Moffat and Mesa Counties), throughout Utah, to westernmost Nye and southern Mineral Counties, Nevada and central Inyo County, California; from ca. 400 (in southern Washington) to 6,600 ft. alt.

Vouchers for chromosome number (5 individuals, 5 populations), $n=14$:

U.S.: CALIFORNIA: INYO CO.: 2.5 mi. N. of Big Pine, R17860. LASSEN CO.: U.S. Hwy. 395, 32 mi. S. of Milford, R17870. IDAHO: FREMONT CO.: 4.8 mi. E. and 2.5 mi. N. of St. Anthony, R19561. NEVADA: ORMSBY CO.: Just E. of New Empire, R17864. OREGON: HARNEY CO.: 12.9 mi. S. of Narrows, R18449.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S. CALIFORNIA: INYO CO.: 2.8 mi. N. of Big Pine, R13825 (DS); 4 mi. W. of Lone Pine, 4,700 ft., *Alexander & Kellogg* 2786 (UC, mixture with *C. pusilla*); head of Division Creek road, 6,500 ft., *Kerr* in 1938 (CAS); foothills W. of Bishop, *Heller* 8288 (CAS, DS, F, GH, NY, PH, UC, US, WS). LASSEN CO.: Secret Valley, *Applegate* 8930 (DS, RSA); 10 mi. S. of Amadee, 4,000 ft., *Jones* in 1897 (POM). MONO CO.: Long Valley, *Noldecke* in 1938 (CAS); near Benton, *Eastwood & Howell* 9547 (CAS, mixture with *C. pusilla*). COLORADO: MESA CO.: Grand Junction, *Eastwood* in 1892 (OSC). MOFFAT CO.: 5 mi. W. of Maybell along Cedar Springs draw, *Weber* 5450 (COLO, DS). IDAHO: COUNTY UNKNOWN: Lannans Spur, *Henderson* 5339 (DS). CASSIA CO.: Raft R., *Davis* 8–37 (IDS). GOODING CO.: 3 mi. S. of Hagerman, *Davis* 1950 (IDS, POM, UC). JEROME CO.: Blue lakes 1893, *Palmer* 74 (US). OWYHEE CO.: N. of Bruneau, *Ripley & Barneby* 6503 (CAS); Indian Cove near Hammett, *Christ* 9533 (NY); Bruneau, *Christ* 4483 (NY). TWIN FALLS CO.: W. of Buhl, *Piemeisel* 40–211 (WTU). NEVADA: ELKO CO.: 2 mi. S. of Contact, *Holmgren* 949 (WS); Toana Range, 5 mi. E. of Shafter, *Maguire* 16892 (NY, mixture with *C. pusilla*). ESMERALDA CO.: Candelaria, *Shockley* 247 (DS; F, mixture with *C. pusilla*; JEPS). HUMBOLDT CO.: 10 mi. N. of Winnemucca, 4,500 ft., *Breene* 185 (POM). NYE CO.: Tonopah, *Shockley* 147 (DS, POM), Twin R., 6,000 ft., *J. M. & M. A. R. Linsdale* 858 (CAS); 10 mi. S. of Calloway, 4,900 ft., *Ripley & Barneby* 3633 (CAS). ORMSBY CO.: Carson City, 5,000 ft., *Jones* in 1897 (POM); Steamboat Springs, *Stokes* in 1903 (UC). WASHOE CO.: 2.1 mi. NE. of Pyramid, 4,100 ft., *Simontacchi* 553 (RSA, UC). OREGON: HARNEY CO.: 21 mi. N. of Frenchglen, *Hitchcock & Muhlick* 21204 (WTU); Narrows, *Peck* 6963 (GH); Squaw Butte, *Steward* in 1956 (OSC); 3 mi. S. of Frenchglen, *Peck* 25205 (UC). LAKE CO.: Alkali L., *Peck* 19440 (CAS); near Summer L., 1,360 m, *Eggleston* 6861 (NY, US). MALHEUR CO.: Near Harper Ranch, 900 m, *Leiberg* 2108 (UD). UTAH: BEAVER CO.: Beaver Mts., near Milford, 4,900 ft., *Stokes* in 1903 (US). GRAND CO.: Thompsons Spring, *Jones* in 1891 (POM). SALT LAKE CO.: Antelope I., 4,300 ft., *Watson* in 1869 (GH, NY, US). SANPETE CO.: Sevier Bridge, *Jones* in 1880 (POM, US). TOOELE CO.: Gold Hill, *Jones* in 1891 (F, NY, POM, RM); Deep Creek, *Jones* in 1891 (F, GH, POM, UC, US). UINTAH CO.: 2 mi. S. of Jensen, 4,700 ft., *Graham* 9019 (POM); between Dinosaur National Monument and Green River, 4,800 ft., *Graham* 7739 (POM). WASHINGTON CO.: Silver Reef, 2,500 ft., *Jones* 5149n (POM). WASHINGTON: FRANKLIN CO.: Pasco, *Piper* 2965 (WS, mixture with *C. pusilla*; GH specimen is all *C. pusilla*). OKANAGAN CO.: Nespelem Road at Hopkins Canyon, *Fiker* 1874 (WS). YAKIMA CO.: Near North Yakima, *Henderson* in 1892 (WTU); Donald Pass, Rattlesnake Hills, *Hoover* 5789 (UC). WYOMING: CARBON CO.: Sierra Madre, *Nelson* in 1907 (RM); Ft. Steele, 6,500 ft., *Tweedy* 4432 (NY, US). SWEETWATER CO.: Granger, *Nelson* 4760 (NY), 4698 (RM, US); Point of Rocks, 6,550 ft., *Ripley & Barneby* 7922 (CAS). TETON CO.: Pacific Creek, *Merrill & Wilcox* 602 (GH, NY, RM, US). WASHAKIE CO.: W. of Worland, 4,100–4,300 ft., *Nichols* 380 (RM).

Camissonia parvula is closely related to *C. pusilla* and *C. pubens* and grows sympatrically with both species. It is the only species of sect. *Camissonia* in Wyoming and Colorado and the most widespread one in Idaho and Utah. It can usually be distinguished readily by its linear leaves, lack of a definite basal rosette, and strigose pubescence, but the plants are occasionally subglabrous or very rarely have a few spreading longer trichomes, in which cases they are difficult to dis-

tinguish from the diploid *C. pusilla* that occurs in the same general areas in northern Nevada and eastern Washington and Oregon. *Camissonia parvula* has also been found growing sympatrically with *C. contorta*.

44. Camissonia campestris (Greene) Raven, Brittonia 16: 284. 1964.

Slender, erect or decumbent annual, usually well branched, with wiry stems and no definitely defined basal rosette, the plants 5–25 (–50) cm. tall, glabrous, hirsutulous, strigulose, or glandular-pubescent; stems with a conspicuously exfoliating white rhytidome. Leaves linear to narrowly elliptic or narrowly oblanceolate, 0.5–2.5 (–3) cm. long, 0.1–0.15(–0.5) cm. wide, sparsely serrulate to coarsely serrate, the apex acuminate, the base attenuate. Inflorescence glandular-pubescent, sometimes very sparsely so or glabrous, or with an admixture of longer eglandular trichomes, or strigulose, sometimes densely so, or sparsely short-villous. Hypanthium 1.5–5.5 mm. long, 2.5–6 mm. across at the summit, more or less densely villous in lower half within, often with a red dot at the summit within at the base of each filament. Sepals 3–8 (–12) mm. long, 1.3–3 mm. wide, reflexed in pairs. Petals (3.5–) 5–15.5 mm. long, (3–) 5–13 mm. wide, usually with two (or one) red dots at the base of each one. Filaments of the episepalous stamens (1.4–) 2.1–5.5 mm. long, those of the epipetalous ones (0.7–) 1.2–3.2 mm. long; anthers 1–2.4 mm. long. Style (3.2–) 4–12 (–15) mm. long, glabrous or sparsely hirsutulous near the base; stigma 0.7–3 mm. in diameter, held well above the anthers at anthesis. Capsule 2–4.3 cm. long, 0.7–1.5 (–2) mm. thick, subsessile. Seeds 0.8–1.6 mm. long, 0.4–0.6 mm. thick. Gametic chromosome number, $n=7$. Self-incompatible.

Distribution (Figure 57): Open sandy flats, endemic to California; often abundant and covering large areas, from the vicinity of Antioch, Contra Costa County, San Joaquin County and northern Stanislaus County, California, south in the San Joaquin Valley, inner Coast Ranges, and Sierra Nevada foothills to Santa Barbara, Ventura, the northern half of Los Angeles, and western Riverside County; near Campo, San Diego County (*Eastwood* 9447, CAS); and western borders of the Mojave Desert from the vicinity of Twentynine Palms and the Little San Bernardino Mountains in northern Riverside and southern San Bernardino Counties northwest to the vicinity of Daggett and Calico, east of Barstow, San Bernardino County, the area about Red Mountain, in westernmost San Bernardino and easternmost Kern Counties, and the southwesternmost corner of Inyo County, where it extends north almost to Olancha. Not found near the coast, and occurring from near sea level on the lower San Joaquin River to about 6,400 ft. alt., in the Sierra Nevada of Kern County. I have also seen a collection from Painted Canyon, in the northwestern corner of the Colorado Desert, Riverside County (*Randall* 219 SD); the

occurrence of *Camissonia campestris* at this locality should be confirmed by additional collections, as should the following: Santa Cruz Mountains, 2,300 ft., *Pendleton* 945 (UC); Panamint Mountains, Inyo County, *Winblad* in 1937 (CAS). Collections of this species cited from the Sacramento Valley and bordering mountains are all polyploid and here referred to *C. lacustris* and *C. contorta*; otherwise all material cited by Munz (Bot. Gaz. 85:258–260. 1928) under *Oenothera dentata* var. *campestris*, var. *johnstonii* (except for collections cited above as *Camissonia kernensis* subsp. *gilmanii*), and var. *parishii* belongs here, and specifically to *Camissonia campestris* subsp. *campestris*.

This species has usually been referred to the South American *Camissonia dentata*, and consequently known as *Oenothera dentata* Cav.; all South American populations, however, are tetraploid ($n=14$ or 13) and self-compatible, the stigma being surrounded by at least the anthers of the longer stamens at anthesis.

44a. Camissonia campestris subsp. **campestris**

Oenothera dentata sensu auct. Amer. bor. mult.; non Cav. 1798.

Oenothera campestris Greene, Fl. Francisc. 216. 1891.

Sphaerostigma campestre (Greene) Small, Bull. Torrey Cl. 23: 189. 1896.

Sphaerostigma campestre var. *parishii* Abrams, Fl. Los Angeles 272. 1904. Type: Plains, San Bernardino, San Bernardino Co., Calif. May 1900, *S. B. Parish* (DS).

Oenothera torulosa race *helianthemiflora* H. Lév., Monogr. Onoth. 178, *pl.* 1905. Lectotype: Mojave Desert, Calif., May 1882, *S. B. & W. F. Parish* 1304 (MO).

Sphaerostigma campestre var. *helianthemiflorum* (H. Lév.) A. Nels., Bot. Gaz. 40: 57. 1905.

Oenothera torulosa f. *permixta* H. Lév., Monogr. Onoth. 180. 1905. Type: Fresno, Fresno Co., Calif., 21 March 1889, collector unknown (presumably MO).

Oenothera dentata var. *campestris* (Greene) Jeps., Man. Fl. Pl. Calif. 685. 1925.

Oenothera dentata var. *parishii* (Abrams) Munz, Bot. Gaz. 85: 259. 1928.

Oenothera dentata var. *johnstonii* Munz, Bot. Gaz. 85: 259. 1928. Type: Near Mojave, Kern Co., Calif., 5 May 1920, *I. M. Johnston* (POM 8844).

Sphaerostigma dentata subsp. *campestris* (Greene) Johansen, Amer. Journ. Bot. 16: 597. 1929.

Oenothera campestris subsp. *campestris* Munz, N. Amer. Fl. II. 5: 158. 1965.

Oenothera campestris subsp. *parishii* (Abrams) Munz, Fl. N. Amer. II. 5: 158. 1965.

Oenothera cruciata sensu Munz, N. Amer. Fl. II. 5: 157. 1965; pro parte.

Plants usually erect; leaves linear to narrowly elliptic or narrowly oblanceolate, serrulate. Gametic chromosome number, $n=7$. Self-incompatible.

LECTOTYPE: California, 1831–2, *D. Douglas* (GH); cf. Munz, Bot. Gaz. 85: 258. 1928.

DISTRIBUTION (Figure 57): That of the species.

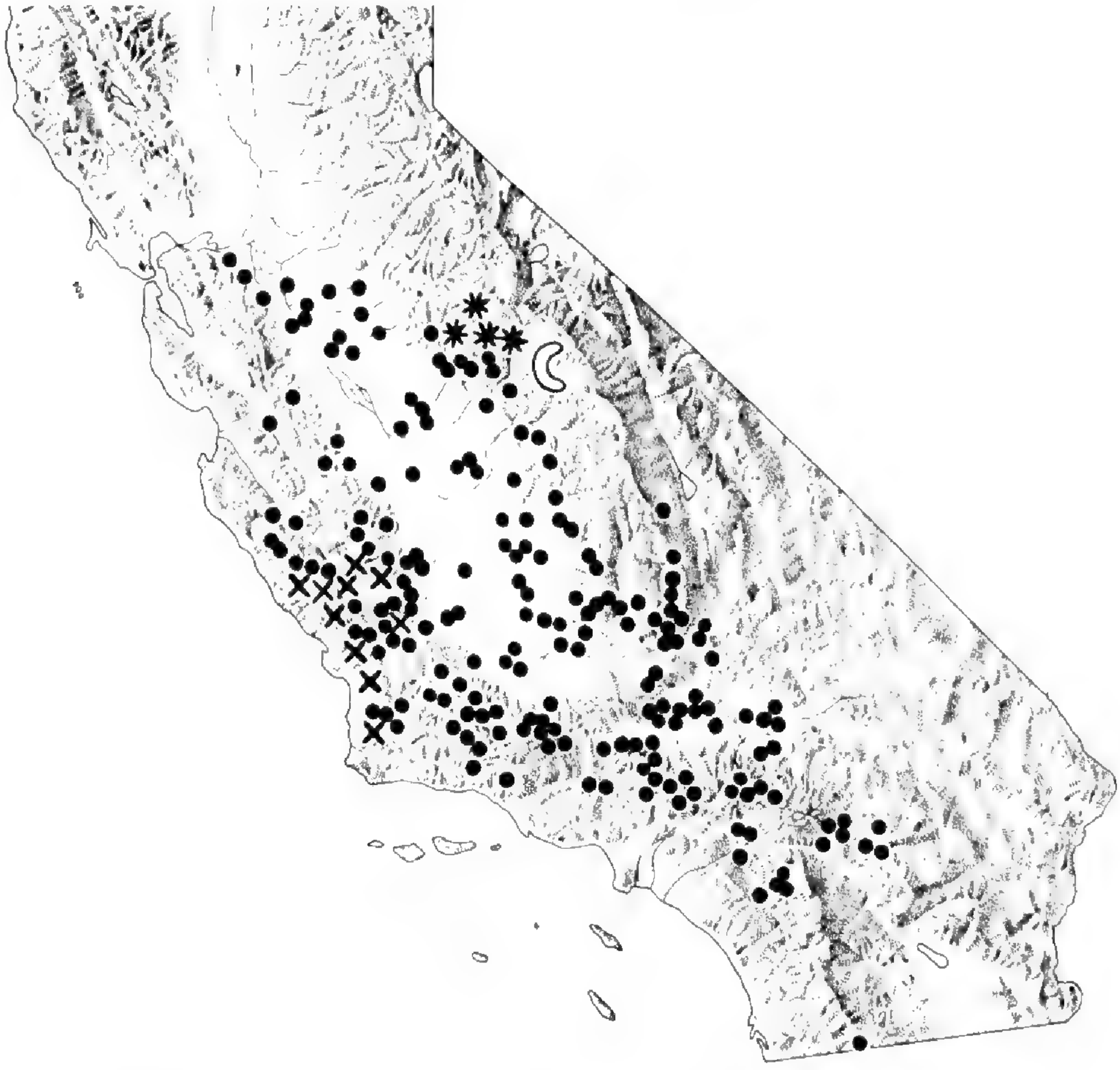


FIGURE 57.—California, showing ranges of species of *Camissonia* sect. *Camissonia:* ● = *C. campestris* subsp. *campestris;* × = *C. campestris* subsp. *obispoensis;* ✳ = *C. sierrae* subsp. *sierrae; C. sierrae* subsp. *alticola*, area outlined by heavy black line.

Vouchers for chromosome number (35 individuals, 32 populations), $n=7$ (all with 7 pairs, except where noted):

U.S.: CALIFORNIA: FRESNO CO.: 3.3 mi. N. of Selma, R17064; 7 mi. SW. of Tollhouse, *Breedlove* 5199. KERN CO.: Jawbone Canyon, *Munz & Gregory* 23310 (RSA); 1.2 mi. SE. of Blackwells Corner, 650 ft., R16982; 0.7 mi. S. of Taft, 800 ft., *Breedlove* 1947; Wheeler Ridge, E. of Maricopa, *Lewis* 1684 (LA); 7.3 mi. N. of Bakersfield, R17078; S. of Arvin, 450 ft., R17089; near mouth of Kern R. canyon, *Lewis et al.* 1675 (LA; 5 pairs + ring of 4); W. of mouth of Kern R. canyon, *Lewis* 1683 (LA; 5 pairs + ring of 4); Kern R. canyon, 8.2. mi above road to Redwood Meadow, *Lewis & Wedberg* 1109 (LA, RSA; two plants, 7 pairs; one, 5 pairs + ring of 4); 8.9 mi. S. of Weldon, R12802; Miracle Hot Springs, R18804; ca. 5 mi. S. of Walker Basin on road to Caliente, *Lewis* 1253; 10 mi. N. of Red Rock Canyon, *Munz & Gregory* 23313 (RSA); Black Mt. burn, Greenhorn Mts., 3,500 ft., R18765; head of Short Canyon, R13985. LOS ANGELES CO.: 0.5 mi. E. of Pearblossom, *Lewis* 1691 (5 pairs + chain of 3 + univalent); 3.7 mi. W. of Littlerock, *Theobald* 88; 1 mi. W. of Littlerock, R13994. MADERA CO.: 7.6 mi. S. of Coarsegold, 1,300 ft., R18330; San Joaquin Experimental Range, between Coarsegold and O'Neals, *Lewis* 1296 (2 plants). MONTEREY CO.: 6 mi. N. of Mission San Antonio, *Breedlove* 5579; 1.5 mi. W. of Bradley, R18205. SAN BERNARDINO CO.: 0.3 mi. N. of junction of Hwy. 138 with Hwy. 395, *Wedberg* in 1957 (LA); Barstow, R11894. SAN LUIS OBISPO CO.: 0.4 mi. S. of San Juan Creek S. of Shandon, 1,150 ft., R16973; 5.5 mi. S. of Shandon on San Juan Creek, 1,200 ft., R16967; 8.6 mi. W. of Simm-

ler, 1,800 ft., *Breedlove* 2061; W. edge of Carrizo Plain, *Breedlove* 2085. SANTA BARBARA CO.: 11.8 mi. W. of New Cuyama, 2,100 ft., *Breedlove* 1939. TULARE CO.: 2 mi. S. of Tipton, 500 ft., R17063.

Two early reports of chromosome number in this species were made by Johansen (Proc. Nat. Acad. Sci. U.S. 15: 884. 1929) but no localities or vouchers were cited.

Plants of this taxon are abundantly visited by oligolectic bees, especially *Andrena* spp. The following populations were found to consist of self-incompatible individuals: 7.6 miles south of Coarsegold, 1,300 ft., Madera County, R18330 (nine plants, tested in field); Black Mountain burn, Greenhorn Mountains, 3,500 ft., Kern County, R18765 (one plant, in greenhouse); 1.5 miles west of Bradley, Monterey County, R18205 (12 plants, tested in field); 3 miles southwest of Livingston, Merced County, R18809 (12 plants, tested in field).

Populations of *Camissonia campestris* from the foothills of the Sierra Nevada tend to have relatively small flowers; but these plants are probably all self-incompatible, judging from the results with the Madera County population mentioned above. Some populations from relatively high elevations in the Greenhorn and Tehachapi Mountains of Kern County consist of plants with relatively broad leaves, but the leaves are attentuate at the base and the plants do not closely resemble *C. sierrae* from farther north. Such collections are (all from Kern County, California): Black Mountain burn, Greenhorn Mountains, 3,500 ft., R18765 (self-incompatible; see above); Wagy Creek Fire Road, east side of Greenhorn Mountains, *Hardham* 3682a (LA); east slope of Bear Mountain, Tehachapi Mountains, 6,200 ft., *Twisselmann* 9633 (DS). The status of these plants should be further investigated.

Oenothera cruciata, as recognized by Munz (N. Amer. Fl. II. 5: 157. 1965), consists of a mixture of late-season plants of *Camissonia campestris* subsp. *campestris*, whence the chromosome count, $n=7$; relatively large-flowered plants of the hexaploid *C. contorta;* and the Clear Lake, Lake County, California, populations of the tetraploid *C. lacustris*.

Hybridization between *Camissonia campestris* and the hexaploid *C. contorta* was studied 1.5 miles due west of Bradley, Monterey County, California, on April 20, 1963. Here both parents were common on a sunny, west-facing hillside in open oak woodland, with *C. campestris* predominant in the more sandy localities and *C. contorta* everywhere. Widely scattered intermediate individuals made up a very small proportion of the population, with some 15 collected among many thousands of the parents. Ten of these were studied cytologically, with observations of meiosis possible in eight. Of these, five had

$2n=28$ chromosomes and were presumably F_1 individuals. The maximum configuration observed was a chain of 8 chromosomes, a ring of 4, two chains of 4, and 4 pairs, two of which were ring bivalents and two heteromorphic rod bivalents. Less extensive chromosome configurations were observed in most cells of most plants, with trivalents rather frequent and univalents occasional. These observations clearly show that the complete lack of multivalent formation in the hexaploid is under genetic control, which breaks down in the hybrids. Pollen stainability in these presumed F_1 individuals was as follows (samples of 200 grains): 0 percent (one plant), 15.5 percent, 20.5 percent, 22.5 percent, 42 percent.

The remaining three plants on which chromosomal observations were made had $2n=21$ and were presumably backcross individuals with *C. campestris* as the recurrent parent. One of these had a ring of 4 chromosomes, a chain of 4, 6 pairs (including 3 ring pairs), and a univalent, with 7 percent stainable pollen; the second had a chain of 4, a chain of 3, 6 pairs, and 2 univalents, with 0.5 percent stainable pollen; and the third had 2 chains of 3, 7 pairs, and a univalent, with 4 percent stainable pollen. The petals in these plants were 5–5.5 mm. long, instead of 4–4.5 mm. as in the presumed F_1 individuals. Despite their low fertility, these individuals strongly suggest the possibility of interspecific hybridization enhancing the variability of *C. campestris*. It is not surprising that no backcrosses with *C. contorta* were obtained in this small sample, for *C. contorta* is largely autogamous, *C. campestris* self-incompatible and outcrossing. Thus backcrossing to *C. campestris* is far more likely than to *C. contorta*.

Another apparent F_1 hybrid plant was studied from 2.9 miles east of Paso Robles, San Luis Obispo County, California, *Keck* 2110 (DS). This completely pollen-sterile individual was mounted on a herbarium sheet with plants of the putative parents. Another similar mixed collection with one apparent F_1 hybrid was collected about 1 mile southeast of Havilah, Kern County, California, 975 m., *Coville & Funston* 1082 (US).

An unusual individual that was presumably not of hybrid origin is *S. B. & W. F. Parish* 1304A (GH), collected with normal individuals of *C. campestris* (1304). In this plant, the petals are narrowed greatly in their upper two-thirds, thus resembling an exaggerated form of the sort of petals found occasionally in *C. hirtella* (sect. *Holostigma*).

Camissonia campestris subsp. *campestris* grows sympatrically with *C. kernensis* subsp. *kernensis*, *C. kernensis* subsp. *gilmanii*, *C. strigulosa*, *C. integrifolia*, and *C. contorta*. It is one of the only two diploid species in that part of sect. *Camissonia* in which the sepals are reflexed in pairs, and thus may have contributed to the origin of the tetraploids *C. lacustris*, *C. benitensis*, *C. strigulosa*, *C. dentata*, and *C. integrifolia*;

these species have very likely had a common origin at the tetraploid level. Judging from the fact that the hexaploid *C. contorta* occupies the hot, dry San Joaquin Valley of California, almost to the exclusion of the tetraploid *C. strigulosa*, which is restricted to the foothills and margins of the valley, it appears likely that *C. contorta* (at least in this area) is an allohexaploid combining genomes from the diploid *C. campsteris* (abundant with it in the valley) and the tetraploid *C. strigulosa*. Whether the hexaploid populations found north and east of the area of *C. campestris* originated in this way or by the functioning of an unreduced gamete in a tetraploid plant cannot at present be determined. It is likely, however, considering the sort of pairing observed in natural hybrids between the diploid *C. campestris* and the hexaploid *C. contorta*, that a hexaploid formed by the functioning of such an unreduced gamete would be pair-forming, and therefore probably fertile, from the time of its origin.

44b. Camissonia campestris subsp. **obispoensis** Raven, subsp. nov.

A subsp. *campestri* differt: foliis anguste ellipticis, grosse serratis; ramis persaepe decumbentibus. Chromosomatum numerus gameticus, $n=7$.

TYPE: Opening in chaparral on sandy soil, 1.8 miles west of Bee Rock, San Luis Obispo County, California, 5 May 1963, *P. H. Raven* 18301 (DS 520310).

DISTRIBUTION (Figure 57): Marine sand deposits in openings in chaparral and oak woodland, endemic to central coastal California from southern Monterey County through northern and western San Luis Obispo County to northwesternmost Santa Barbara County; from ca. 300–1,600 ft. alt.

Vouchers for chromosome number (5 individuals, 5 populations), $n=7$:

U.S.: CALIFORNIA: MONTEREY CO.: E. edge of San Antonio Valley, Santa Lucia Mts., 1,350 ft., *Breedlove* 2268; Bradley, R18306; Big Sandy Valley 2 mi. N. of Indian Valley Road, R18290. SAN LUIS OBISPO CO.: 1.8 mi. W. of Bee Rock, R18301; Atascadero, R18278.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: MONTEREY CO.: Big Sandy, N. of San Miguel, *Hardham* 10823 (DS); Big Sandy, 3 mi. NE. of Indian Valley, N. of San Miguel, *Hardham* in 1962 (DS); Lowes Canyon, 15 mi. N. of San Miguel, *Hardham* 3332 (CAS, LA), R18296 (DS); ca. 3 mi. N. of summit of Hog Canyon Road S. of Parkfield, R18300 (DS); Cholame Creek (upper end), *Jepson* 15903 (JEPS); 28.1 mi. NE. of San Miguel, Big Sandy to Parkfield road, *Hardham* 10773 (DS, RSA). SAN LUIS OBISPO CO.: Nacimiento Dam to Bradley-Pleyto road, *Hardham* 4582 (SBBG); Cantinas Creek, near N. end of Nacimiento L., *Hardham* 4567 (LA, SBBG); sand dunes on top of Tierra Redonda, *Hardham* 1859 (LA, SBBG); 1.6 mi. W. of Bee Rock, *Hardham* 2259 (LA); 5 mi. ESE. of Bryson, 1,500 ft., *Graham* 379 (UC); Oak Flat Road intersection with road to Adelaida, *Hardham* 2058 (LA); upper

Navajo Creek, *Hoover* 6898 (CAS); Yaro Creek district N. of Pozo, *Hoover* 6993 (CAS); Chimney Rock Ranch, South Road to Adelaida, *Hardham* 829 (LA); Santa Margarita, *Summers* in 1886 (ARIZ, POM), *Wall* in 1933 (CAS, POM); upper Arroyo Grande, *Hoover* 6860 (CAS, RSA); road from Arroyo Grande to Huasna, *Eastwood* 14988 (CAS). SANTA BARBARA CO.: 3 mi. NE. of Mt. Solomon, 800 ft., *Lee* 241 (UC); Cuyama Valley, *Pollard* in 1953 (CAS, RM).

This distinctive local endemic intergrades completely with subsp. *campestris* wherever the ranges of these two taxa approach one another. A series of hybrids between *C. campestris* subsp. *obispoensis* and *C. strigulosa* is represented by *Hardham* 3240 (LA, RSA, SBBG), from a damp grain field at Bee Rock, northern San Luis Obispo County, California. The fertility of four representative putative F_1 hybrids, based on the stainability of a sample of 200 pollen grains from each in cotton blue in lactophenol was, respectively, 11, 1.5, 6.5, and 9 percent. A similar population is represented by *Hardham* 10823 (DS), from the Big Sandy, north of San Miguel, 21.2 miles north of the Salinas River bridge, Monterey County, California, where it grew on the borders of the road. This collection includes two plants of *C. campestris* subsp. *obispoensis*, one of *C. strigulosa*, and two hybrids, one of which had a pollen stainability of 0.5 percent, based on a sample of 200 pollen grains.

An apparent backcross to this subspecies from a hybrid between it and the hexaploid *C. contorta* was found with the presumed parents at Atascadero, San Luis Obispo County, California (R18281). This individual had 7 pairs of chromosomes, 3 univalents, and a chain of 4; it was not setting any seed.

45. Camissonia sierrae Raven, sp. nov.

Herba annua hirsutulosa humilis, plerumque ramis multis e basi; caules tenuissimi, ad 15 cm. longi. Folia lanceolata vel anguste ovata, aliquando elliptica, 0.5–1.8 cm. longa, 0.2–0.5 cm. lata, subintegria, apice acuta, basi rotundata vel obtusa. Inflorescentia pilis glandulosis brevioribus admixta. Hypanthium 1.3–2.2 mm. longum, ostio 1.2–2.2 mm. diametro, intus in dimidio inferiore hirsutulosum, summum puncto rubro prope basin omnium filamentorum. Sepala 3–4.2 mm. longa, 1–1.3 mm. lata, binatim reflexa. Petala 4–7 mm. longa, 3.5–5 mm. lata, unumquidque prope basin punctis duabus rubris maculatum. Filamenta staminorum episepalorum 2.4–3.2 mm. longa, illa epipetalorum 1.2–2 mm. longa; antherae 0.6–1.2 mm. longae. Stylus 4.5–7 mm. longus; sub anthesi insuper antheribus minime portatum vel antheris staminorum longiorum stigma 0.6–0.8 mm. diametro, circumnexum. Capsula tenuissima, 2–3 cm. longa, ca. 0.5–0.7 mm. crassa, sessilis. Semina his *C. campestris* similia. Chromosomatum numerus gameticus, $n=7$. Plus minusve autogama.

TYPE: Meadow in forest dominated by *Pinus ponderosa*, 0.7 miles west of junction in Oakhurst on road to Mariposa, 2,400 ft., Madera

County, California, 7 May 1963, *P. H. Raven* 18343 (DS; isotypes, BM, GH, NY, RSA, US).

DISTRIBUTION (Figure 57): Carpeting the ground locally in open forest of *Pinus ponderosa* and at the upper limits of the *Pinus sabiniana–Quercus douglasii* forest, from 1,800–4,000 ft. alt., Sierra Nevada foothills of central California, in central Mariposa and Madera Counties.

Vouchers for chromosome number (2 individuals, 2 populations) $n=7$.

U.S.: CALIFORNIA: MADERA CO.: 0.7 mi. W. of Oakhurst, R18343 (type collection); 4.3 mi. W. of Oakhurst, R18345.

ADDITIONAL SPECIMENS EXAMINED:

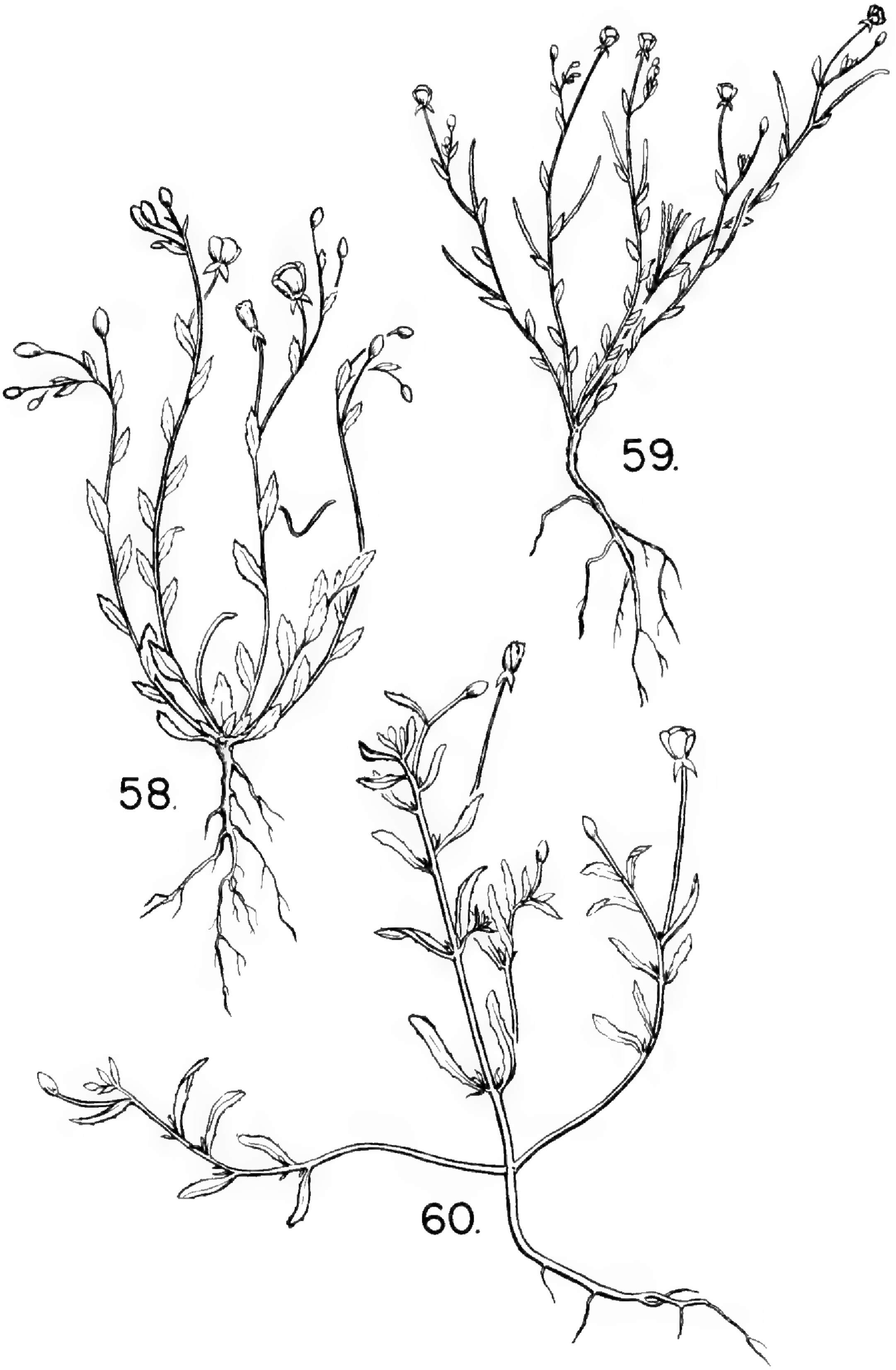
U.S.: CALIFORNIA: MADERA CO.: 3.7 mi. W. of Oakhurst, *Thorp* 63–10 (DS); S. end of Oakhurst, *Thorp* 63–12 (DS); the Falls, Bass Lake, 3,450 ft., *H. & M. Dearing* 5955 (DS, SBBG); Bass Lake, *H. & M. Dearing* 6018 (SBBG, UCSB). MARIPOSA CO.: Yosemite Valley, *Corring* in 1884 (GH), *Bioletti* in 1900 (NY), *Head* in 1906 (CAS), 4,000 ft., *Wright & Patchett* in 1917 (JEPS); Royal Arches, Yosemite Valley, *Jepson* 10478 (DS, JEPS); Little Yosemite, *Flinn* in 1925 (F); 2 mi. off state highway, 7 mi. below Mariposa on road to Ben Hur, 1,800 ft., *Wolf* 4836 (COLO, POM, RSA, SD, WS, WTU).

Camissonia sierrae is a delightful and distinctive endemic found above the upper limits of *C. campestris*, its closest relative, in the central Sierra Nevada of California. The latter species occurs locally in much drier habitats. Eighteen plants of *Thorp* 63–10, cited above, were tested for pollen-tube growth and found to be self-compatible, in contrast to all known populations of *C. campestris*. Despite this, *C. sierrae* is probably outcrossed to a large extent, and is abundantly visited by bees, including a large species of *Andrena* (*Onagrandrena*). Its stigma is often held above the anthers and this, together with the red markings at the summit of the hypanthium and on the petals, is highly correlated with outcrossing in *Camissonia*, as is the abundant pubescence in the lower half of the hypanthium within and near the base of the style.

This species is very probably a derivative of *C. campestris*, but is usually easily distinguished by its habit (cf. fig. 58) and much broader, relatively shorter leaves. The populations from Mariposa County have narrower leaves and a laxer habit than those from Madera County, but form a distinctive morphological and ecological unit with them. *Camissonia sierrae* has been observed growing sympatrically with *C. contorta* at the type locality of the former.

45a. Camissonia sierrae subsp. **sierrae** FIGURE 58

All of the preceding remarks apply to this subspecies. It has been necessary in this instance to depart from the usual format of this paper, as both subspecies are being described as new at this time.



FIGURES 58–60.—Species of *Camissonia* sect. *Camissonia*, × ¾: 58, *C. sierrae* subsp. *sierrae* (*Raven* 18343, holotype, DS); 59, *C. sierrae* subsp. *alticola* (*Russell* 75, DS); 60, *C. benitensis* (*Raven* 15084, holotype, DS).

45b. Camissonia sierrae subsp. **alticola** Raven, subsp. nov. FIGURE 59

A subsp. *sierrae* differt: floribus parvioribus; hypanthio 1–2.2 mm. longo, ostio 0.9–2.2 mm. diametro, intus subglabro; sepalis 1.2–3 mm. longis, 0.8–1.5 mm. latis; petalis 2.2–4 mm. longis, 1.8–2.2 mm. latis, immaculatis; filamentis staminorum episepalorum 1.8–2.8 mm. longis, illis epipetalorum 0.8–1.8 mm. latis; antheris 0.6–0.9 mm. longis; stylo 2.8–5 mm. longo, glabro; stigmate 0.6–0.8 mm. diametro, sub anthesi antheris circumnexo. Chromosomatum numerus gameticus, $n=7$. Autogama.

TYPE: Grassy pocket of soil in seepage over granite ledge 100 yards north of Mono Hot Springs Campground, in yellow pine forest, 6,500 ft., Fresno County, California, 8 June 1963, *D. E. Breedlove* 5212 (DS; isotypes, BM, GH, NY, RSA, US).

DISTRIBUTION (Figure 57): Shallow soil on granite outcrops, yellow pine forest, in the Sierra Nevada of northeastern Fresno County, California, from 6,500–7,700 ft. alt.

Voucher for chromosome number (1 individual, 1 population), $n=7$:

U.S.: CALIFORNIA: FRESNO CO.: Mono Hot Springs, *Breedlove* 5212 (type collection).

ADDITIONAL SPECIMENS EXAMINED:

U.S.: CALIFORNIA: FRESNO CO.: Near Bear Dam, 7,300 ft., R7157 (CAS); Mono Hot Springs, 6,500 ft., R6217 (CAS), *S. & C. H. Quibell* 2326 (DS), *Ferguson* 430 (DS, JEPS); between Florence L. and Blaney Meadows, 7,500 ft., R4284 (CAS); Florence L., *Russell* 75 (DS); 3/8 mi. above E. end of Vermillion Valley, ca. 7,700 ft., *C. H. & E. M. Quibell* 2670 (herb. Fresno State College).

A distinctive local race, *Camissonia sierrae* subsp. *alticola* is obviously very closely related to *C. sierrae* subsp. *sierrae* but is highly autogamous and occurs at much higher elevations. I have seen a collection from Lake Merced on the Merced River of Mariposa County, 7,200 ft., *Jepson* 3181 (JEPS), which is very similar to Fresno County plants of subsp. *alticola;* additional collections from the Merced River drainage basin would make it possible to evaluate the relationship between these two series of populations.

46. Camissonia lacustris Raven, sp. nov. FIGURE 61

Oenothera dentata var. *campestris* sensu Munz, Bot. Gaz. 85: 258. 1928; pro parte.

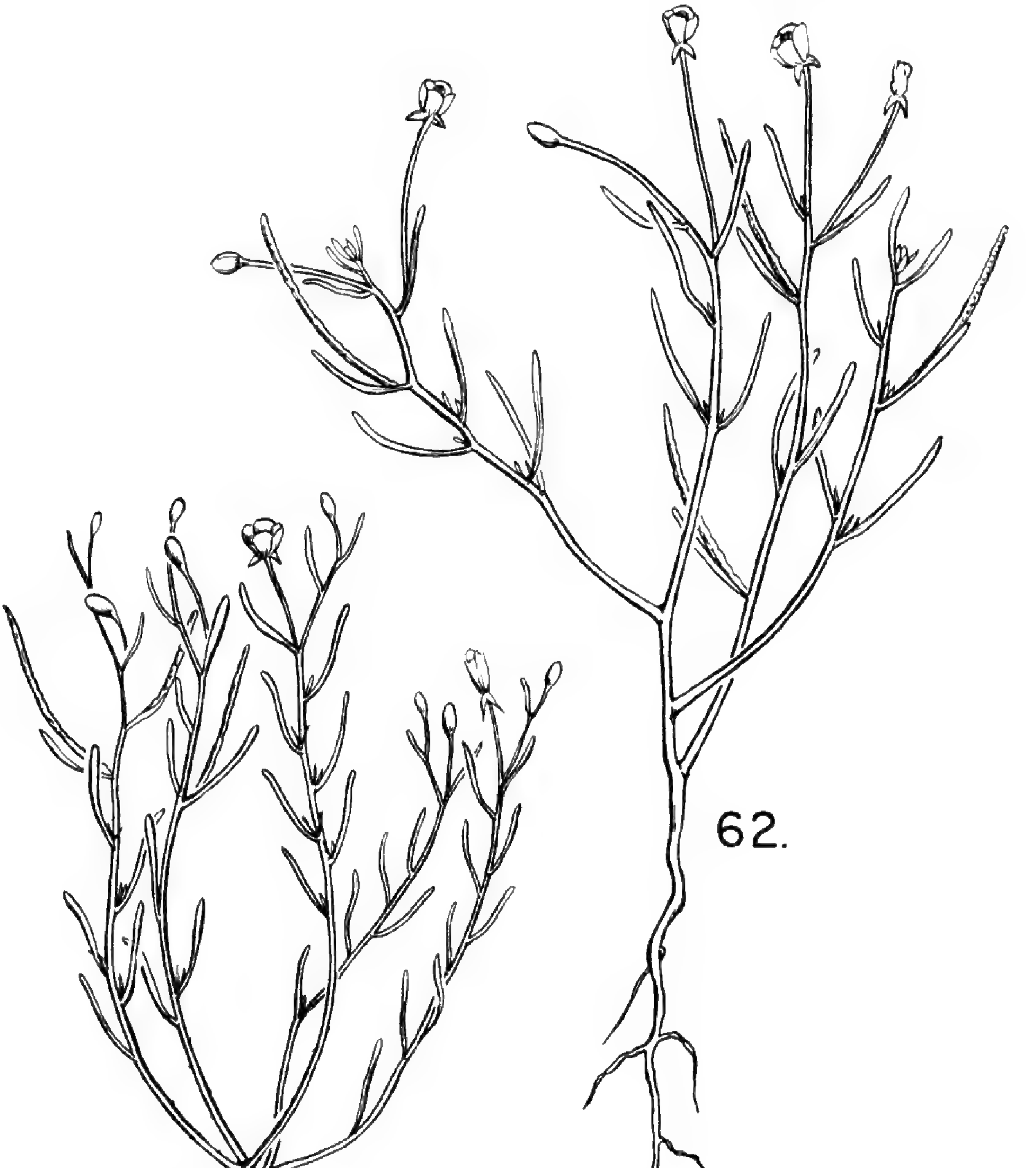
Oenothera contorta var. *epilobioides* sensu Munz, Bot. Gaz. 85: 256. 1928; pro parte.

Oenothera dentata sensu Munz, N. Amer. Fl. II. 5: 157. 1965; pro parte.

Oenothera cruciata sensu Munz, Amer. Fl. II. 5: 157. 1965; pro parte.

Oenothera campestris subsp. *campestris* sensu Munz, N. Amer. Fl. II. 5: 158. 1965; pro parte.

Herba annua *C. strigulosae* persimilis. Plantae pilis longis erectis dense vestitae; inflorescentia glanduloso-pubescens. Hypanthium intus in partem dimidiam pubescens. Sepala (3–) 3.8–5.5 mm. longa.



FIGURES 61–62.—Species of *Camissonia* sect. *Camissonia*, × ¾: 61, *C. lacustris* (*Raven* 18164, holotype, DS); 62, *C. integrifolia* (*Raven* 12806, holotype, DS).

Petala (4–) 4.5–7 mm. longa, (2.8–) 3–6.5 mm. lata, plerumque unumquidque prope basin punctis duabus rubris maculatum. Filamenta staminorum episepalorum 2.5–3.5 mm. longa, illa epipetalorum 1.7–2.5 mm. longa; antherae 0.8–1.3 mm. longae. Stylus (3.5–) 4–7 mm. longus, prope basin pubescens. Chromosomatum numerus gameticus, $n=14$. Autogama.

TYPE: In open grassland of serpentine hill 0.2 mile west of State Highway 29 near Lakeport, Lake County, California, 13 April 1963, *P. H. Raven* 18164 (DS).

DISTRIBUTION (Figure 63): Open grassland of central California, in two disjunct areas: serpentine soil along the northwest side of Clear Lake, Lake County, 1,400–1,800 ft. alt.; Sierra Nevada foothills from Eldorado to Fresno County, 600–5,000 ft., scattered.

Vouchers for chromosome number (5 individuals, 4 populations), $n=14$:

U.S.: CALIFORNIA: LAKE CO.: 0.2 mi. W. of Lakeport, R18164 (type collection), *Breedlove* 4546. MARIPOSA CO.: Bootjack Road at Chowchilla School, 2,900 ft., R18346. TUOLUMNE CO.: 1 mi. NE. of Tuolumne City, *Breedlove* 4817; Carnegie Institution Field Station, Mather, *Lewis* 1665 (LA, RSA).

FIGURE 63.—California, showing ranges of some tetraploid ($n=14$) species of *Camissonia* sect. *Camissonia:* northern limits of the widespread *C. strigulosa* indicated by a dotted line; ○=*C. lacustris*, with ●=tetraploid chromosome counts; ✳=*C. benitensis;* △=*C. integrifolia*, with ▲=tetraploid chromosome count.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: CALAVERAS CO.: Mokelumne Hill, *Blaisdell* (GH, US). ELDORADO CO.: N. fork of the Cosumnes R. NW. of Youngs, R9107 (CAS, RM). FRESNO CO.: Pine Flat, 600 ft., *C. H. & E. Quibell* 1712 (NY, RSA); 4 mi. W. of Pine Ridge, *Breedlove* 5275 (DS). LAKE CO.: Cold Creek Canyon, 1,800 ft., *Schulthess* in 1928 (POM); near Lakeport, *Baker* 3067 (CAS, NMC, POM, UC); Kelseyville, *Blankinship* in 1923 (RSA). MARIPOSA CO.: Near Leconte Memorial, Yosemite Valley, 4,000–4,500 ft., *Abrams* 4426 (DS, GH, NY); Camp Curry, *Stone* in 1915 (PH); Little Yosemite, *Smith* in 1908 (ARIZ, PH). TUOLUMNE CO.: Hog Ranch, Hetch-Hetchy Valley, 4,700 ft., *Grant* 974 (POM); Phoenix L., *Grant* 946 (JEPS).

Camissonia lacustris is very closely related to and probably derived from the widespread tetraploid *C. strigulosa*. The latter occurs in the Sierra Nevada north only to Kern County and in the North Coast Ranges only on the immediate coast to the vicinity of Bodega Bay. Thus *C. lacustris* occupies a series of widely scattered enclaves in the area now within the range of the hexaploid *C. contorta*. It is of interest that the northernmost population of tetraploids in this section in the Coast Ranges, that near Clear Lake, Lake County, occurs on serpentine: marginal populations of plants often occur on substrates unusual for the species as a whole, and such a situation is ideal for the derivation of edaphically restricted endemics (cf. Raven, Evolution 18: 336–338. 1964). In *Camissonia contorta*, the hexaploid which occurs in the same areas, often a third or more of the pollen grains are 4-pored, whereas in *C. lacustris* and other tetraploids of sect. *Camissonia* it is rare for as many as 5 percent of the pollen grains to be 4-pored. The long, spreading trichomes on the stems of *C. lacustris* and its relatively large flowers are likewise useful in its recognition.

In the vicinity of Clear Lake, Lake County, California, *Camissonia lacustris* occurs on serpentine soils and the hexaploid *C. contorta* nearby on the nonserpentine soils now under moderately heavy cultivation. The records of *C. campestris* (*Oenothera dentata* auct.) from Lake County apply to *C. lacustris*, as do some of the populations included in Munz' (N. Amer. Fl. II. 5: 157. 1965) concept of *Oenothera cruciata* (S. Wats.) Munz, a diverse assemblage of unrelated elements with several different chromosome numbers. Twelve individuals from the type locality were selfed in the field and found to be self-compatible by pollen-tube growth; the stigma is surrounded by at least the anthers of the four longer stamens even in the largest flowered individuals of this species.

47. Camissonia benitensis Raven, sp. nov. FIGURE 60

Herba annua *C. strigulosae* persimilis. Plantae 3–18 mm. altae, plus minusve purpurascentes, ramis secondariis tenuibus numerosis ad angulum 90° patentibus, pilis longis 0.2–0.3 mm. longis erectis

dense vestitae; inflorescentia glanduloso-pubescens et villosa. Folia angustissime elliptica, sparsa, 0.7–2 cm. longa, 0.15–3 cm. lata, apice acuta. Hypanthium ca. 1.2 mm. longum ostioque diametro, intus in partem dimidiam dense brevipubescens. Sepala 3.2–3.5 mm. longa, ca. 1.5 mm. lata. Petala 3.5–4 mm. longa, ca. 3 mm. lata, unumquidque prope basin punctis duabus rubris maculatum. Filamenta staminorum episepalorum ca. 2 mm. longa, illa epipetalorum ca. 1.2 mm. longa, unumquidque basi puncto rubro. Stylus 2.1–2.5 mm. longus, glaber; stigma sub anthesi antheribus circumnexum. Chromosomatum numerus gameticus, $n=14$. Autogama.

TYPE: On serpentine by small stream 5.4 miles from Hernandez on road to New Idria, along Clear Creek, San Benito County, California, 19 April 1960, *P. H. Raven* 15084 (DS; isotype, US).

DISTRIBUTION (Figure 63): Clay soils derived from serpentine, lower Clear Creek Drainage, San Benito County, California, at an elevation of ca. 2,000 ft.

ADDITIONAL SPECIMEN EXAMINED:

U.S.: CALIFORNIA: SAN BENITO CO.: Along wash of Clear Creek 1.8 mi. from Hernandez on road to New Idria, R15094 (DS).

This distinctive species is apparently an endemic of serpentine soils in the vicinity of the type locality. Nonserpentine soils in the vicinity are occupied by populations of the hexaploid *Camissonia contorta*, which species tends to occur in light sandy soil, and expecially along washes. Both of the collections of *C. benitensis* cited above were tetraploid, with 14 pairs of chromosomes at meiotic metaphase I. Like *C. lacustris*, it occupies an enclave in an area that is now dominated by the hexaploid, and, also like *C. lacustris*, it was probably derived from *C. strigulosa*.

48. Camissonia strigulosa (Fisch. & Mey.) Raven, comb. nov.

Sphaerostigma strigulosum Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 50. 1835.
Oenothera strigulosa (Fisch. & Mey.) Torr. & Gray, Fl. N. Amer. 1: 512. 1840.
Oenothera strigulosa var. *epilobioides* Greene, Fl. Francisc. 216. 1891. Lectotype: Near Los Angeles, Los Angeles Co., Calif., 1890, *A. Davidson* (ND).
Sphaerostigma contortum var. *greenei* Small, Bull. Torrey Cl. 23: 189. 1896; nom. subs.
Oenothera contorta var. *strigulosa* (Fisch. & Mey.) Munz, Bot. Gaz. 85: 255. 1928.
Oenothera contorta var. *epilobioides* (Greene) Munz, Bot. Gaz. 85: 256. 1928.
Oenothera dentata sensu Munz, Fl. N. Amer. II. 5: 157. 1965; pro parte.

Erect or sometimes decumbent annual, to 5 dm. tall, usually well branched, with wiry stems and no well-defined basal rosette, the stems white or later brown, with exfoliating rhytidome; plants strigulose and often also glandular-pubescent, especially in the inflorescence, or occasionally glandular-pubescent only and then subglabrous;

hirsute pubescence sometimes present near the base, but this almost always accompanied by strigulose pubescence higher on the stems. Leaves linear to very narrowly elliptic, 0.8–3.5 cm. long. 0.1–0.3 cm. wide, sparsely serrulate. Hypanthium 1.6–2.7 mm. long, 1.1–2.4 mm. across at the summit, moderately to very sparsely pubescent within in lower half, or more rarely glabrous. Sepals 1.6–4 mm. long, 1–1.65 mm. wide, reflexed in pairs, the short tips of the sepals subterminal and distinct in bud. Petals 2.1–4.2 (–4.5) mm. long, 1.4–3.1 mm. wide, sometimes with two red dots at the base of each one. Filaments of the episepalous stamens 0.9–2 (–2.2) mm. long, those of the epipetalous ones 0.5–1.3 mm. long; anthers 0.3–0.6 mm. long. Usually less than 10 percent of the pollen with four pores. Style 2.3–4.8 mm. long, pubescent or rarely glabrous near the base; stigma 0.8–1.4 mm. in diameter, surrounded by the anthers of both sets of stamens at anthesis, and these shedding pollen directly on the stigma. Capsule straight or somewhat flexuous, 1.5–4.5 cm. long, 0.8–1.3 mm. thick, subsessile, with a sterile beak usually 1.5–3 mm. long. Seeds 0.6–0.8 mm. long, 0.3–0.4 mm. thick. Gametic chromosome number, $n=14$. Autogamous.

LECTOTYPE: Sphaerostigma strigulosum F. M. California. Cult.—C. A. Meyer" (ex herb. Ledebour), LE. This specimen closely matches a modern collection from the dunes between the town of Bodega Bay and Bodega Head, Sonoma County, California, *Raven* 18246, which is known to be tetraploid. It was probably grown from seeds gathered in the vicinity of Fort Ross, Sonoma County, California, at the northern limit of the species.

DISTRIBUTION (Figure 64): Widespread in open sandy grassland, vicinity of Bodega Bay, Sonoma County, California, south through the Coast Ranges to the vicinity of Santa Eulalia, at about 30°43′ N. lat. in Baja California; common in cismontane southern California, and in the Tehachapi Mountains, through which it reaches the southern Sierra Nevada of Kern County, California; Santa Rosa Island. A single collection supposed to be from Fort Huachuca, Arizona, has been seen, but the presence of this species in Arizona should be confirmed; this collection might represent a short-term introduction, for example. From sea level to 6,700 ft. alt.

Vouchers for chromosome number (54 individuals, 50 populations), $n=14$:

U.S.: CALIFORNIA: KERN CO.: Near Havilah, R18802; 1 mi. S. of Havilah, *Lewis* 1345, 3.4 mi. S., R20251; 0.5 mi. W. of Weldon, R18799 (sympatric with *C. contorta*); Weldon, R18777 (sympatric with *C. integrifolia*), 18796 (sympatric with *C. contorta*); 5 mi. S. of Weldon, R18793 (sympatric with *C. integrifolia*); 9.7 mi. S. of Weldon, 3,100 ft., R17561; NE. of Lake Isabella, 2,600 ft., *Howell* 37164 (CAS; progeny=R18844, 19750); Black Mt. burn, Greenhorn Mts., 3,500 ft., *Howell* 38215 (CAS; progeny=R18784; sympatric with *C. campestris* and

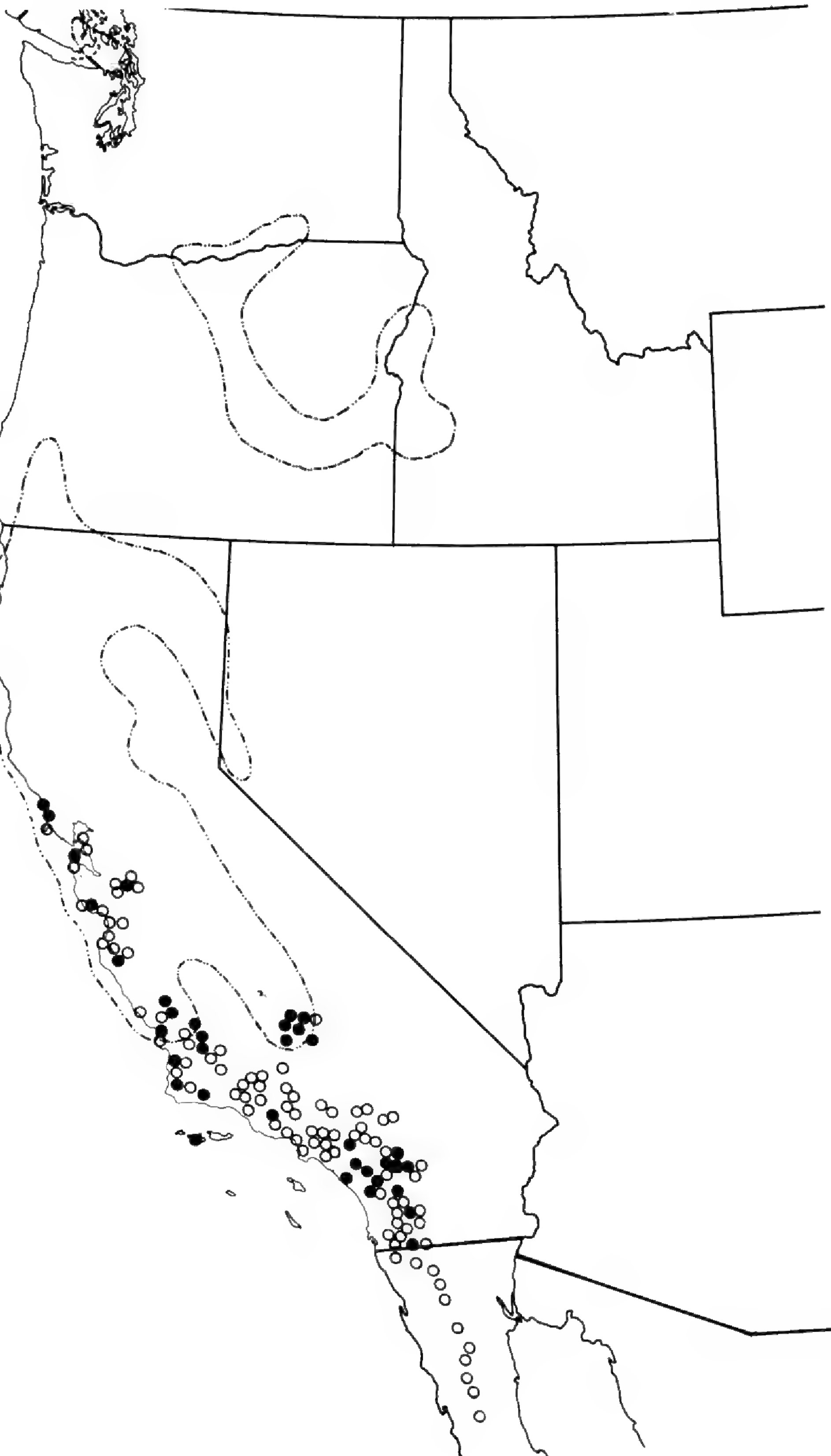


FIGURE 64.—Western United States and a portion of northwestern Mexico: ○=range of *Camissonia strigulosa*, with ●=tetraploid chromosome counts ($n=14$); area of the closely related hexaploid *C. contorta* is outlined with dotted line.

C. contorta). MARIN CO.: Dillons Beach, R18244. MONTEREY CO.: Paloma Creek, road from Arroyo Seco to Jamesburg, R18217; Big Sandy Valley, R18282. ORANGE CO.: 5.6 mi. NE. of Mission San Juan Capistrano, *Wedberg* 179. RIVERSIDE CO.: Reche Canyon, *Wedberg* 228; 4.1 mi. W. of Dripping Springs, R14022; Cajalco Road 0.1 mi. W. of Mockingbird Canyon Road, *Wedberg* 197; Machado Road near Elsinore, *Wedberg* 192; 7.7 mi. E. of Hemet, *Wedberg* 199 (herb. San Diego State College); 1.8 mi. S. of Hemet, *Wedberg* 201 (herb. San Diego State College); San Jacinto River wash 2.1 mi. SW. of Cranston Ranger Station, San Jacinto Mts., *Lewis* 1250; Hemet Meadows, San Jacinto Mts., R14245; Lake Fulmor, San Jacinto Mts., R14234; Vanderbilt Flat, San Jacinto Mts., *Wedberg* in 1957 (LA, RSA). SAN DIEGO CO.: Warner Hot Springs, *Kuijt* in 1958 (progeny); Dodge Valley, *Wedberg* 225 (herb. San Diego State College); 2.5 mi. W. of Julian, *H. & M. Lewis* 1672 (LA); 2.4 mi. N. of Pala, R16919; 2.2 mi. W. of Campo R16925. SAN FRANCISCO CO.: Sunset District, *Breedlove* 4907. SAN LUIS OBISPO CO.: 4.5 mi. E. of Santa Margarita, R20159; 8.6 mi. W. of Simmler, La Panza Range, 1,800 ft., *Breedlove* 2059; Morro Bay, R17935; Nipomo Mesa, *Breedlove* 2099, 4267, R17956; Camatti Creek, R18322; 2.9 mi. E. of San Miguel, R18311; Simmler to Creston Road, 3.6 mi. W. of junction with Pozo to Simmler Road *H. & M. Lewis* 1609 (LA); summit of road between Arroyo Grande and Edna, *Lewis et al.* 1664 (LA). SANTA BARBARA CO.: 4 mi. N. of Lompoc, R15509; Juncal Campground, upper Santa Ynez Valley, 1,800 ft., *Breedlove* 2234; E. of Torrey Pines, Santa Rosa I., R15000. SANTA CLARA CO.: Upper Arroyo del Puerto, Mt. Hamilton Range, R18231, *Breedlove* 4890. SANTA CRUZ CO.: Summit of Quail Hollow Road near Ben Lomond, R18184; 1 mi. S. of Ben Lomond, *Breedlove* 4636. SONOMA CO.: Between town of Bodega Bay and Bodega Head, R18246. VENTURA CO.: Cow Spring Campground, 17.6 mi. N. of Fillmore, Topatopa Mts. 3,500 ft., *Breedlove* 2645.

BAJA CALIFORNIA: 7.5 mi. N. of Santo Tomás, R17048.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: ALAMEDA CO.: Alameda, *Jepson* in 1891 (JEPS, NY, UC US); Oakland, *Brewer* 2735 (US). CONTRA COSTA CO.: West Berkeley, *Tidestrom* in 1893 (POM). FRESNO CO.: Priest Valley to Parkfield Junction, *Thomas* 497 (DS; all pollen 3-pored). KERN CO.: Miracle Hot Springs, *Buckalew* 23 (RSA); Cuddy Valley, near Mt. Pinos, 5,500 ft., *Hall & Chandler* 6356 (UC); W. end of Tecuya Ridge, 6,800 ft., *Twisselmann* 9577 (CAS, DS); Black Bob Canyon, 4,200 ft., *Twisselmann* 8339 (CAS, DS); Kernville, 2,650 ft., *Howell* 37114 (CAS); Temblor Range W. of McKittrick, *Eastwood & Howell* 4099 (CAS). LOS ANGELES CO.: Browns Flat, San Gabriel Mts., 4,300 ft., *Wheeler* 915 (CAS, LA, UC); near Inglewood, *Abrams* 3237 (DS, GH, LE, NMC, NY, PH, POM, UC, US); vicinity of Elizabeth Lake, 2,750 ft., *Hall* 3051 (DS, NY, POM, RM, UC, US; possibly *C. contorta*, and one individual with 40 percent 4-pored pollen); summit Mt. Wilson, 6,000 ft., *Grant* in 1906 (DS); Tuna Canyon, Verdugo Hills, *MacFadden* in 1931 (GH, NY, RM, UC); Santa Monica Mts., 800 ft., *Abrams* 1261 (DS, NY, POM); Tujunga Creek at Barley Flats Trail crossing, 4,046 ft., *Ewan* 7271 (POM). MARIN CO.: Dunes near the radio station, Pt. Reyes Peninsula, *Howell* 21755 (CAS). MONTEREY CO.: Tassajara Hot Springs, 1,550 ft., *Ferris* 8314 (DS, GH, UC); Pacific Grove, *Patterson & Wiltz* in 1907 (DS); near Soledad, *Howitt* 1510 (CAS); San Simeon, *T. S. Brandegee* in 1888 (UC). ORANGE CO.: Rancho Santa Ana, 500 ft., *Howell* 900 (RSA). RIVERSIDE CO.: Banning, 2,300 ft., *Jones* in 1903 (DS, POM); Temescal Canyon, 8 mi. SE. of Corona, *Hitchcock & Muhlick* 22136 (DS, UC, WS, WTU); Idyllwild, San Jacinto Mts., 5,400 ft., *Spencer* 2201 (POM). SAN BENITO CO.: San Juan Bautista, *Brewer* 715 (UC). SAN BERNARDINO

co.: San Bernardino Valley, *S. B. & W. F. Parish* 81 (DS, F, GH, NY, UC, US); N. of Cajon Pass, 3,600 ft., *Peirson* 4514 (RSA); Mojave R. at Deep Creek, 3,000 ft., *Lewis* 1428 (LA); Redlands, *Lewis* in 1937 (LA); Baldwin Lake, 6,700 ft., *Munz* 10745 (POM, UC). SAN DIEGO CO.: 2 mi. E. of Pala, *Munz* 10371 (POM); Warner Springs, 3,132 ft., *Rose* 49097 (COLO, RSA); Palomar Mt., 6,000 ft., *Cooper* 1494 (NY); pasture between Middle and South Peaks, Cuyamaca Mts., 5,000 ft., *Munz* 9792 (DS, POM); Descanso, *Munz & Harwood* 7137 (GH, POM, RM, UC); Jacumba, *Munz* 8091 (POM); Campo, *Eastwood* 9383 (CAS); base of San Miguel Mt., *Gander* in 1935 (POM). SAN FRANCISCO CO.: Presidio, Lake Merced, *Rose* 41282 (ARIZ, C, CAS, COLO, DS, GH, LA, NMC, NY, OSC, PH, POM, RM, UC, US, WS); Sutter St., San Francisco, *Rattan* in 1878 (DS). SAN LUIS OBISPO CO.: Salinas R. 5 mi. N. of Paso Robles, *Wiggins* 3421 (DS); Queen Bee Public Camp, La Panza Range, 2,300 ft., *Munz* 16325 (NY, RSA, WTU); Price Canyon, *Hoover* 9171 (CAS); Pismo Beach, *Abrams* 6513 (DS); foothills of Caliente Mt., Carissa Plains, *Hardham* 1786 (LA); Black Lake, S. of Arroyo Grande, *Hoover* 7069 (CAS, RSA). SAN MATEO CO.: South San Francisco, *Eastwood* in 1894 (GH); Colma, *K. Brandegee* in 1905 (UC). SANTA BARBARA CO.: Santa Barbara, *Elmer* 4001 (CAS, COLO, DS, F, GH, NY, POM, US); 10 mi. W. of Buellton, *Munz* 10297 (C, POM); base of Figueroa Mt., *Breedlove* 209 (UCSB); Big Pine, San Rafael Mts., *Hoffmann* in 1929 (CAS); E. fork of Lion Canyon, below Pine Corral Potrero, Sierra Madre Mts., 4,500 ft., *Blakley & Muller* 3425 (CAS, DS, JEPS, SBBG, UCSB; might be *C. contorta*); near edge of Pine Corral Potrero, near Salisbury Potrero, 4,500 ft., *Muller & Blakley* 1015 (DS, SBBG; might be *C. contorta*—22 percent 4-pored pollen); Santa Rosa I., *Brandegee* in 1888 (UC). SANTA CLARA CO.: Mt. Hamilton, *Elmer* 4625 (ARIZ, CAS, DS, NY, OSC, POM, UC, US, WS). SANTA CRUZ CO.: Swanton, *Rick* in 1912 (DS); Sunset Beach State Park, *Thomas* 3073 (DS); near Boulder Creek, ca. 650 ft., *Thomas* 1781 (DS). SONOMA CO.: Bodega Bay, *Heller & Brown* 5613 (COLO, DS, F, GH, NY, PH, POM, RM, US); "Colon Ross," *Wrangell* (LE). STANISLAUS CO.: Head of Adobe Creek, Adobe Valley, 1,600 ft., Mt. Hamilton Range, *Sharsmith* 3564 (RSA, UC). VENTURA CO.: North Fork of Ventura R. 1.7 mi. above Wheelers Hot Springs, 1,900 ft., *Wolf* 6898 (CAS, DS, GH, NY, RSA, UC, WS, WTU); Red Reef Canyon, Topatopa Mts., 2,800–3,500 ft., *Abrams & McGregor* 155 (DS, GH, NY, US); Matilija Canyon area above dam, *Pollard* in 1947 (CAS); Dry Lakes Ridge, Matilija-Sespe Divide, ca. 4,700 ft., *Pollard* in 1962 (CAS).

BAJA CALIFORNIA: 1.5–2.5 mi. upstream from Rincón, 4.5 mi. NE. of Santa Catarina, 64 mi. SE. of Ensenada, ca. 4,100 ft., *Broder* 716 (DS, UCSB); 9 mi. SE. of Tecate, *Munz* 9477 (POM, UC); 15 mi. NNW. of Rosarito, 3,780 ft., *Wiggins* 10009 (DS, US); Laguna Hansen, 5,450 ft., Sierra Juárez, *Gander* 3294 (SD); Rancho San José (Meling's Ranch), 2,300 ft., *Wiggins* 9771 (DS, UC, US); Rancho San Matias, 31°17′N. lat., 115°33′W. long., ca. 1,050 ft., *Moran* 10843 (DS, SD); Santa Eulalia, 30°43′N. lat., 115°20′W. long., ca. 1,850 m, *Moran* 11135 (DS, SD).

Camissonia strigulosa is a tetraploid species very closely related to the South American tetraploid *C. dentata* and at times distinguishable from it only with difficulty. Hybrids between these two species are, however, highly sterile (Raven & Moore, MS.), and most individuals can be distinguished by their habit and flower size, which is often larger in the South American populations. *Camissonia strigulosa* is likewise very closely related to the North American hexaploid *C. contorta*, although the latter can usually be distinguished by its posses-

sion of more than 10 percent 4-pored pollen grains, a character which is of course directly correlated with its higher chromosome number. In Kern County, California, in the southern Sierra Nevada, where the ranges of the two overlap, tetraploid individuals (=*C. strigulosa*) have appressed pubescence on the stems, hexaploid individuals (=*C. contorta*), spreading pubescence. This distinction does not always hold true in the Coast Ranges, but is sometimes useful.

Despite the undoubtedly close relationship between these three species, I prefer to maintain them as distinct, particularly in view of the other closely related but more easily distinguishable entities that are accorded taxonomic recognition in this revision. It is likely that differentiation at the tetraploid level has given rise to the local endemics *C. benitensis* and *C. integrifolia*, and the relatively local *C. lacustris* in North America, and to *C. dentata* following the introduction of a seed of this tetraploid group to South America (cf. Raven, Quart. Rev. Biol. 38: 151–177. 1963). The three relatively uncommon North American tetraploids are now at the margins of the range of the common tetraploid, *C. strigulosa*, and in two cases completely surrounded by populations of the hexaploid. As mentioned in the discussion of the diploid *C. campestris*, it is likely that some populations of the hexaploid *C. contorta* (those in the San Joaquin Valley of California, especially) have originated following hybridization between the diploid *C. campestris* and the tetraploid *C. strigulosa;* others have very probably originated by the occasional functioning of unreduced gametes in tetraploid populations.

Hybridization between *C. campestris* subsp. *obispoensis* and *C. strigulosa* has been mentioned in the account of the former taxon, above. From a bud collection made at Miracle Hot Springs, Kern County, California (R17567), I obtained a meiotic chromosome configuration of ca. 5 weakly joined pairs, a chain of 3 chromosomes, and 22 univalents ($2n=35$), suggesting hybridization between the hexaploid *C. contorta* and the tetraploid *C. strigulosa* at this locality; unfortunately, the individual from which these buds were taken was not identified in the collection. Another individual from the same collection had 5 pairs, a chain of 3 chromosomes, and 8 univalents, suggesting hybridization between *C. campestris* subsp. *campestris*, also present at this locality, and the tetraploid *C. strigulosa*. In addition to the three taxa just mentioned, *C. strigulosa* also has been observed growing sympatrically with the tetraploids *C. pubens* (*Munz* 13357, RSA) and *C. integrifolia*; hybridization with the latter is discussed under the treatment for that species, and with the diploid *C. kernensis* subsp. *kernensis*.

A single collection of what appears to be this species is supposed to have been made at Fort Huachuca in southern Arizona (May

1892, *Wilcox,* NY; Trans. N.Y. Acad. Sci. 14: 37. 1894). If the collection is properly labeled, the plant may have been a temporary introduction at this locality, perhaps with feed for animals; it is not otherwise known from Arizona.

49. Camissonia dentata (Cav.) Reiche, Fl. Chile 2: 264. 1898.[3]

South American plants very similar to the North American *C. strigulosa,* but differing in most cases by a combination of the following characteristics. Plants ascending, decumbent, or prostrate. Leaves linear to broadly elliptic, 0.3–2.8 cm. long, 0.07–0.45 cm. wide, usually denticulate but more rarely subentire. Hypanthium 0.8–3 mm. long. Sepals 1–4(–5) mm. long, 0.7–2 mm. wide. Petals 1.5–6(–8) mm. long. Filaments of the episepalous stamens 0.5–1.8 mm. long, those of the epipetalous ones 0.5–1.3 mm. long; anthers 0.5–1.3 mm. long. Style 0.8–5 mm. long; stigma 0.5–0.8 mm. thick, usually surrounded by the anthers in anthesis, but elevated above them in the plants with the largest flowers. Capsule 0.8–3.5 cm. long, 0.6–1.3 mm. thick. Seeds 0.8–1.1 mm. long, 0.3–0.5 mm. thick. Gametic chromosome numbers, $n=14$, 13. Self-compatible and usually autogamous.

DISTRIBUTION: In South America, from Arequipa, Peru, southward west of the Andes to Concepción Province, Chile, and southeastward in Argentina to Lago Argentino and Deseado in Gobernación de Santa Cruz. From sea level to ca. 3,500 ft. alt. throughout most of its area, but in northernmost Chile and southern Peru mostly between ca. 9,500 and 12,500 ft. alt. A map of the range of this species will be given by Raven and Moore (MS.).

The extreme variability of this complex species, which occupies a north-south range of some 2,500 miles in South America, has been the basis of a great deal of taxonomic confusion. The two recent treatments of the South American members of *Camissonia* (Munz, Physis 11: 266–292. 1933; Farm. Chil. 3–12. 1934) divide the populations here assigned to this species into five taxa: *Oenothera contorta* var. *divaricata* (Gay) Munz, *O. contorta* var. *epilobioides* (Greene) Munz, *O. dentata* Cav. (var. *dentata*), *O. dentata* var. *campestris* (Greene) Jeps., and *O. micrantha* var. *acuminata* (Phil.) Munz. *Camissonia cheiranthifolia,* erroneously reported from Chile in its protologue by Gay (Fl. Chile 2: 330. 1846) and by Reiche (Fl. Chile 2: 263. 1898), was correctly excluded from the flora of South America by Munz (Farm. Chil. 10. 1934; Rev. Univ. Cat. Santiago 22: 275. 1937). Munz distinguished *Oenothera dentata* from *O. contorta* on the basis of the larger flowers of the former, with petals 4–7 mm. long, those of

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[3] The treatment of this species is by P. H. Raven and D. M. Moore, Department of Botany, The University, Leicester, England. Moore's fieldwork in Chile and Argentina was supported by grants from the National Science Foundation to Harlan Lewis and from the Royal Society of London to Moore.

the latter given as 2.5–3.5 mm. long. In our study of a wide range of Chilean material, however, we have found a complete range of flower size, the petals ranging from 1.5–6 or even 8 mm. long. With one exception, this variation does not appear to be geographically correlated. Collections from the central part of Concepción Province tend to have larger flowers than those from elsewhere, although plants with petals longer than 3 mm. are scattered from Coquimbo to Concepción. Sample measurements of petal length are given in the list of cited specimens.

Munz (1933–34, 1937) separated *Oenothera contorta* var. *divaricata* from var. *epilobioides* on the basis of the larger size and longer capsules of the latter, which often had a sterile tip at the apex. We have been unable, however, to confirm these relationships in our studies of South American material. Neither have we found the nature of the pubescence to be a reliable or geographically correlated characteristic. Many of the plants in this group have glandular pubescence in the inflorescence, but a large number have strigose pubescence, and these two types are sometimes found mixed in a single gathering. Other plants are subglabrous.

Oenothera dentata var. *campestris* was separated from *O. dentata* in Munz' treatment of the Chilean species (1934) by its narrower leaves. Such plants are sporadic throughout central Chile and ought not to be confused with the California diploid *Camissonia campestris* for reasons which will be made clear below.

Finally, as regards *Oenothera micrantha* var. *acuminata*, we have seen only a photograph made of the type in Santiago (GH). The plant shown is exceptional in its long-acuminate upper leaves, but in other respects there seems to be no reason why it could not be an unusual form of the complex so widespread throughout South America. It certainly seems unreasonable, on the basis of this single specimen, to credit the North American sect. *Holostigma* to South America. It is, however, highly desirable that similar plants be re-collected, and they may exist in Bíobío or neighboring provinces.

Despite the fact that all of the South American populations of this genus seem to belong to a single species, there are two distinctive geographical races within this species that deserve formal taxonomic recognition. The more local and uniform series of populations consists of a group of heavyset, broad-leaved plants with relatively large flowers and thick, heavy capsules found along the coast of Concepción and the neighboring provinces. This series is described as *C. dentata* subsp. *littoralis*.

We have grown 15 populations of this species, including 2 populations of subsp. *littoralis*, in the experimental garden. Of these, 13 had $n=14$, and 2, one belonging to the series of relatively large-

flowered populations from Concepción mentioned above and the other to subsp. *littoralis*, had $n=13$. The two populations with $n=13$ represent the only naturally occurring aneuploid populations in the genus, but they are not strongly separated by sterility barriers from other South American populations with $n=14$. A summary of our cytogenetic and experimental studies with this group is given elsewhere (Raven & Moore, MS).

It appears likely that *Camissonia* may have reached South America only once, and relatively recently, by long-distance dispersal across the tropics (Raven, Quart. Rev. Biol. 38: 151–177. 1963), a phenomenon which has probably occurred twice in *Gayophytum*, once in *Clarkia*, and twice in *Boisduvalia*, three other genera of annual plants in the Onagraceae. *Camissonia dentata* is obviously most closely related to the North American tetraploid *C. strigulosa*, from which it may well have been derived, but the South American entity is far more variable, and most populations can easily be distinguished from those of North America. In these respects, the situation is closely similar to that in *Clarkia*. In view of this, the high degree of sterility between North and South American plants (Raven & Moore, MS) and the degree of morphological distinction between the species recognized in North America in this assemblage, it appears best to consider the North and South American plants as specifically distinct. If this is not done, the oldest name for the collective group would be *Camissonia dentata*, a name which (as *Oenothera dentata*) has usually been incorrectly applied to the diploid species here called *Camissonia campestris* in North America. Should *Camissonia dentata* be understood in this collective sense, it would probably be best to include the hexaploid *C. contorta* in the same species, but it would probably still be possible to maintain the more local tetraploids *C. benitensis* and *C. lacustris* as species distinct from this complex. *Camissonia integrifolia*, a third local tetraploid species, is so distinct morphologically that it does not really enter into this problem.

49a. Camissonia dentata subsp. **dentata**

Oenothera dentata Cav., Icon. 4: 67, *t. 398*. 1797, excl. verbis falsis "stigma . . . quadrifidum, laciniis ovatis minimis."

Camissonia flava Link, Jahrb. Gewachsk. 186. 1818.

Oenothera chamissonis Link, Enum. Pl. Hort. Berol. 1: 378. 1821. Type: Chile, presumably cultivated at Berlin, and probably destroyed (not seen).

Holostigma argutum Spach, Ann. Nat. Sci. Bot. Paris II. 4: 270. 1835; nom. subs.

Holostigma heterophyllum Spach, Ann. Sci. Nat. Bot. Paris II. 4: 271. 1835; nom. subs.

Sphaerostigma chamissonis (Link) Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 49. 1835.

Holostigma tenuifolium Spach, Ann. Sci. Nat. Bot. Paris II. 4: 270. 1835; non *Oenothera tenuifolia* Cav. 1797. Type: Chile, *Bertero* (P), not seen. The

Unio Itineraria distribution of Bertero's 466 and 1190 (BM, NY, S), from "Quintero, Quillota, in petrosis aridis planitiei fluvii Cachapual," is a mixture of large- and small-flowered plants, probably from two different localities; the small-flowered plants may be isotypes of this species, or the type collection may be *Bertero* 467 (BM), from Rancagua, Prov. O'Higgins.

Oenothera chilensis D. Dietr., Syn. Pl. 2: 1285. 1840; non Fisch. & Mey. 1835.

Oenothera heterophylla (Spach) Steud., Nom., ed. 2, 2: 206. 1841; non Spach 1835, nec Nutt. ex Hook. & Arn. 1838.

Oenothera minutiflora D. Dietr., Syn. Pl. 2: 1285. 1840. Type: Cultivated, from Chile, *C. A. Meyer* (isotype, LE).

Sphaerostigma dentatum (Cav.) Gay, Fl. Chil. 2: 326. 1846.

Sphaerostigma heterophyllum (Spach) Gay, Fl. Chil. 2: 327. 1846.

Sphaerostigma tenuifolium (Spach) Gay, Fl. Chil. 2: 327. 1846.

Sphaerostigma divaricatum Gay, Fl. Chil. 2: 238, *t. 22.* 1846. Type: Sandy places in the low mountains around Santiago, Chile (not seen).

Sphaerostigma ramosissimum Philippi, Linnaea 33: 68. 1864. Type: Near Concumen, Aconcagua, Chile, *Landbeck* (SGO, not seen; photographs, GH, POM).

Sphaerostigma acuminatum Philippi, Anal. Univ. Chile 84: 629. 1893. Type: Sandy places near Nacimiento, Bíobío, Chile, January 1877, *Philippi* (SGO; isotype, NY).

Chamissonia acuminata (Phil.) Reiche, Anal. Univ. Chile 98: 481. 1897.

Chamissonia tenuifolia (Spach) Reiche, Fl. Chile 2: 263. 1898.

Chamissonia paradoxa var. *divaricata* (Gay) Reiche, Fl. Chile 2: 264. 1898.

Oenothera torulosa f. *chilensis* (D. Dietr.) H. Lév., Monogr. Onoth. 180. 1905

Oenothera contorta var. *divaricata* (Gay) Munz, Physis 11: 288. 1933.

Oenothera micrantha var. *acuminata* (Phil.) Munz, Farm. Chil. 11. 1934.

Oenothera dentata var. *campestris* sensu Munz, Farm. Chil. 10. 1934.

Oenothera contorta var. *epilobioides* sensu Munz, Farm. Chil. 10. 1934.

Plants erect, decumbent, or prostrate. Leaves linear or very narrowly lanceolate. Capsules 0.6–0.9 mm. thick. Gametic chromosome numbers, $n=14$, 13. Self-compatible and mostly autogamous.

TYPE: Near Coquimbo and Talcaguano, Coquimbo, Chile, Nov., *Ruiz & Pavon* (MA; photographs, CONC, F). Judging from the photographs I have seen, the flowers are probably shown a little too large in the illustration that accompanies the type description; the stigma was certainly not 4-lobed in this plant.

DISTRIBUTION: That of the species, except coastal Arauco and Cautín Provinces, Chile.

REPRESENTATIVE SPECIMENS EXAMINED:

ARGENTINA: BUENOS AIRES: Carmen de Patagones, *Miccio-Peralta* 67 (DS). CHUBUT: "Río Carren" (?), *Skottsberg* in 1908 (UPS); "Futalenfú," *Skottsberg* in 1908 (S, UPS); Lago Colue Huapi, *Riggs* 67 (F, GH). COMODORO RIVADAVIA: 50 km. W. of town of Lago Buenos Aires, *Eyerdam et al.* 24491 (GH, K, UC). NEUQUÉN: Neuquén, 240 m, *Comber* 37 (K); Río Caliefu, *Cabrera* 5109 (F, POM); Piedra de Águila, 40°02′S. lat., 70°01′ W. long., *Senn* 4244 (RSA); Cerro Lotena, 900 m, *Ammann* 83 (F). Río NEGRO: San Carlos de Bariloche, 800 m, *Buchtein* in 1905 (US); General Roca, 250–360 m, *Fischer* 85 (BM, F, GH, K, NY, US); shore of Lago Nahuel Huapi, *Cordini* 155 (POM, US). SANTA CRUZ: Deseado, *Darwin* 129 (K); Tehuelches, 300 m, *Donat* 87 (BM, F, GH, K, S, UC); 160 km.

S. of Deseado on road to San Julian, *Eyerdam et al.* 23912, (GH, UC); San Julian, 50 m, *Blake* 318 (K); 78 km. S. of San Julian on road to Santa Cruz, Río Chico, *Eyerdam et al.* 23994 (GH, UC); S. shore of Lago Argentino 3 km. E. of Calefate, 270 m, *Eyerdam et al.* 24279 (GH, K, UC).

CHILE: Aconcagua: Papudo, *E. W. D. & M M. Holway* 65 (GH, US); Los Andes, *Mancilla* in 1952 (CONC). Arauco: Isla Santa Maria, *Beck* 75 (K). Atacama: Sandy washes around El Morro, ca. 14 km. ENE. of Caldera, *Worth & Morrison* 16165 (GH, UC); La Varilla, ca. 25 km. N. of Vallenar on road to Capiapó, *Worth & Morrison* 16262 (GH, K, UC); Cachiyuyo, *Ricardi & Marticorena* 4885/1270 (CONC). Bfobfo: Candelaria, Arenales de Los Setenta, *Junge* in 1935 (CONC; petals 5 mm long). Colchagua: La Rufina, Río Claro, *Ricardi* in 1951 (CONC); Talcarihue, San Fernando, *Ricardi* in 1950 (CONC). Concepción: Puente Itata, road from Concepción to Bulnes, *Pfister* 810 (CONC; petals 6.5 mm long); Quilacoya, *Pfister* 298 (CONC; petals 6 mm long); between Yumbel and Estación Yumbel, *Marticorena et al* in 1959 (CONC; petals 4.5 mm long); Pangal del Laja, W. of Yungay, *Marticorena et al.* in 1959 (CONC; petals 3.5 mm long), *Ricardi & Marticorena* 4991/1375 (CONC; petals 5 mm long). Coquimbo: Punta Colorado, *Rose & Rose* 19340 (NY, US); Paihuano, Valle del Cochiguaz, 1,120 m. *Behn* in 1948 (CONC); Parque Lambert, ca. 6 km. NW. of La Serena on road to Islon, 30 m, *Worth & Morrison* 16337 (GH, K, UC); Coquimbo, 30 m, *Elliot* 548 (K; petals 4.5 mm long); Fray Jorge, *Muñoz* B112 (GH); Los Vilos, *Behn* (CONC; petals 3–4 mm long); ca. 5 km. above Los Molles, *Moore* 215 (DS). Curico: Los Queñes, *Milner* 45 (CONC). Malleco: Fundo Tambillo near Nacimiento, *Hempel* 7422 (CONC; petals 6–8 mm long), *Pfister* in 1934 (CONC; petals 2 mm long). Maule: Caquenes, *Reid* (K, NY; some plants with petals 2.5 mm long, others 5.5–6 mm). Ñuble: Fundo Santa Ana, *Behn* in 1937 (CONC); Rfo Cholguan, road from Yungay to Huépil. *Pfister* in 1946 (CONC). O'Higgins: Callanas, Río Pangal valley, *Moore* 263 (DS). Santiago: Batuco, over 500 m, *Looser* 3652 (GH); San Antonio, coast, *Claude-Joseph* 1449 (US); Esmeraldar, Departmento Melpilla, *Reed* 1867/10 (GH). Talca: Talca, *Claude-Joseph* 1692 (US). Tarapacá: Road from Azapa to Chapiquiña, Episcacha, Km. 94, 3,500 m, *Ricardi & Marticorena* 4760/1145 (CONC). Valparafso: Limache, Cuesta La Dormida, 1,200 m, *Behn* in 1940 (CONC); Valparaíso, 60 m, *Sandeman* 202 (BM, K); Viña del Mar, *Buchtein* in 1895 (S). Without definite locality: *Gay* (GH, K, NY, RSA; "*Sphaerostigma tenuifolium* Spach").

PERU: Arequipa: Chachani, 3,350 m, *Stafford* 607 (BM, K); near Chiguata, 3,100 m., *Várgas* 8093 (RSA); Pampa de Arrieros, 3,750 m., *Pennell* 13327 (F, GH, NY, PH); lower slopes of Misti, 3,050 m, *Sandeman* 4002 (K); Tiabaya, 2,100–2,200 m., *Pennell* 13096 (PH). Without definite locality: *Dombey* 726 (F).

49b. Camissonia dentata subsp. **littoralis** Raven & Moore, subsp. nov.

A subsp. *dentata* differt: foliis latioribus, 0.5–1.8 cm. longis, 0.2–0.45 cm. latis, crassioribus; plantis prostratis; capsulis crassioribus, 1.2–2.5 cm. longis, 1.1–1.3 mm. latis. Numerus chromosomatum gameticus, $n=14$, 13. Autogama.

Type: Near Concepción, Concepción, Chile, 1855, *P. H. Germain* (GH; isotypes, BM, F, K). An isotype is illustrated in H. Lév., Monogr. Onoth., facing p. 175. 1905.

Distribution: Sandy soil and dunes on the coast of Concepción, Arauco, and Cautín Provinces, Chile; from sea level to a few hundred feet alt.

SPECIMENS EXAMINED:

CHILE: ARAUCO: Laraquete, *Moore* 290 (DS). CAUTÍN: Bajo Imperial, *Moreton Middleton* in 1906 (BM, S). CONCEPCIÓN: San Vicente, *Scott Elliott* 197 (BM), *Junge* in 1934 (CONC): Concepcíon, *Jaffuel* 2906 (GH), *Cuming* 116 (BM): mouth of the Bíobío, *Ricardi* 8520 (CONC); N. side, mouth of the Bíobío, *Junge* in 1935 (CONC), *Pfister* 297 (CONC), in 1941 (CONC), in 1948 (CONC), *Ramírez* in 1959 (CONC); Tomé, *Junge* in 1935 (CONC); Coronel, *Hill* 167 (K); Coronel, Mina Schwager, *Sparre* 10111 (CONC); Lengua, in mouth of Estero Lengua in Bahía San Vicente, *Moore* 276 (DS). PROVINCE UNKNOWN: Taliahua, *Philippi* (US); I. Quiriquina, *Gunckel* 2805 (GH).

This distinctive and fairly localized entity occupies the southern part of the coastal range of this species in Chile. It has relatively large flowers, the petals ranging from 3–5.5 mm. long.

A specimen from Concepción (*Elliot* 549, GH, K) is spreading in habit but does not have the broad leaves of subsp. *littoralis;* one from San Pedro, Concepción (*Sparre* 14229, CONC) is closer to *littoralis* but intermediate. Likewise, a single collection that has been examined from farther north (Santo Domingo, south of Llolleo, Santiago, *Looser* 1455 GH) approaches subsp. *littoralis*, as does one from Linares, Playa de Pelluhue, *Aravena* 61 (UC, US).

For some unknown reason, Hector Léveillé (Monogr. Onoth. 175. 1905) considered this taxon a species distinct from his *Onothera torulosa*, in which he included all other members of sect. *Camissonia*. He called this species *Onothera hyssopifolia* Molina, Saggio Chile, ed. 2, 134. 1810, but Molina says of his species "fiore . . . terminale violetto, di più d'un pollice di diametro . . ."; it seems likely that, as suggested by Munz (Farm. Chil. 7. 1934), this name refers to some form of *Clarkia tenella* (Cav.) H. & M. Lewis (*Godetia tenuifolia* (Cav.) Spach). *Onothera hyssopifolia*, however, was not mentioned by Moore and Lewis in the most recent revision of the South American species of *Clarkia* (Bol. Soc. Arg. Bot. 10: 332–340. 1965).

50. Camissonia integrifolia Raven, sp. nov. FIGURE 62

Herba annua *C. strigulosae* persimilis. Inflorescentia dense cinereo-strigulosa; plantae sparse strigulosa vel subglabrae. Folia linearia, integria, rare dentibus parvulis obscuris 1–2. Hypanthium intus in partem dimidiam pubescens. Stylus prope basin pubescens vel glaber. Capsula stricta, erecta, 4.5–6 cm. longa. Semina 1–1.2 mm. longa, 0.4–0.5 mm. crassa. Chromosomatum numerus gameticus, $n=14$. Autogama.

TYPE: On bank covered with *Artemisia tridentata*, Weldon, Kern County, California, 3 May 1958, *P. H. Raven* 12806 (DS).

DISTRIBUTION (Figure 63): Dry, often deserty slopes along the Kern River from Miracle Hot Springs to the vicinity of Weldon, Kern County, California; 2,450–3,000 ft. alt.

Vouchers for chromosome number (1 population, 1 individual), $n=14$:

U.S.: California: kern co.: Weldon, R18776 (grown in experimental garden).

Additional specimens examined:

U.S.: California: kern co.: Weldon, 2,450 ft., R17536 (DS), 18791 (DS); mouth of Kelso Canyon at State Hwy. 178, 2,800 ft., *Twisselmann* 7041 (CAS, DS, SBBG); 5 mi. S. of Weldon, R18792 (DS); 6 mi. from Weldon on road to Kelso Valley, 3,000 ft., *Weatherby* 1158 (RSA); 8.3 mi. S. of Weldon on road to Kelso Valley, 2,900 ft., R17560 (DS); Miracle Hot Springs, ca. 2,500 ft., *Buckalew* 23 (RSA).

Camissonia integrifolia is a narrow endemic of a portion of the upper Kern River drainage. It is distinctive in its entire leaves, long, erect capsules, and distribution of its pubescence. *Raven* 17536, cited above, is predominantly this species but includes two plants of *C. strigulosa* and one probable hybrid. A chromosome determination was made of one plant of this collection, which had an extremely irregular polyploid meiosis, suggesting hybridity. Progeny of this collection was grown at Stanford, yielding R18776 (*C. integrifolia*, $n=14$), R18777 (*C. strigulosa*, $n=14$), and R18778, a single obvious hybrid between these two species. The hybrid had variable meiotic configurations ranging from 8 univalents and 10 pairs of chromosomes to 1 chain of 3, 13 univalents, and 6 pairs. It had 11 percent stainable pollen, based on a sample of 200 grains in lactophenol. Thus *C. integrifolia* appears amply distinct from *C. strigulosa*, from which it may have been derived, and grows sympatrically with it, with the occasional formation of sterile hybrids. These two species were also observed growing sympatrically at the locality of R18792, cited above. *Camissonia integrifolia* has also been observed growing sympatrically with *C. kernensis* subsp. *kernensis*, *C. pubens*, *C. campestris*, and *C. contorta*.

51. Camissonia contorta (Dougl.) Kearney, Trans. N.Y. Acad. Sci. 14: 37. 1894.

Oenothera contorta Dougl., *in* Hook., Fl. Bor. Amer. 1: 214. 1834.

Sphaerostigma contortum (Dougl.) Walp., Rep. 2: 78. 1843.

Oenothera dentata var. *cruciata* S. Wats., Proc. Amer. Acad. 8: 594. 1873. Lectotype: Sandy places in the Sacramento Valley, Calif., *Hartweg* 1733 (GH, NY).

Oenothera campestris var. *cruciata* (S. Wats.) Greene, Fl. Francisc. 216. 1891.

Sphaerostigma campestre (Greene) Small var. *minus* ("minor") Small, Bull. Torrey Cl. 23: 189. 1896.

Oenothera cheiranthifolia var. *contorta* (Dougl.) H. Lév., Monogr. Onoth. 216. 1905.

Oenothera torulosa f. *cruciata* (S. Wats.) H. Lév., Monogr. Onoth. 180. 1905.

Oenothera torulosa f. *mixta* H. Lév., Monogr. Onoth. 180. 1905. Type: Possibly at MO; cf. A. Nelson, Bot. Gaz. 40: 57. 1905.

Sphaerostigma campestre var. *mixtum* (H. Lév.) A. Nels., Bot. Gaz. 40: 57. 1905.

Oenothera contorta var. *typica* Munz, Bot. Gaz. 85: 253. 1928.

Oenothera contorta var. *strigulosa* sensu Munz, Bot. Gaz. 85: 255. 1928; pro parte.
Oenothera contorta var. *epilobioides* sensu Munz, Bot. Gaz. 85: 256. 1928; pro parte.
Oenothera contorta var. *contorta*; Munz, N. Amer. Fl. II. 5: 156. 1965.
Oenothera cruciata (S. Wats.) Munz, N. Amer. Fl. II. 5: 157. 1965.
Oenothera dentata sensu Munz, N. Amer. Fl. II. 5: 157. 1965; pro parte.

Very similar to *C. strigulosa*, but almost always with hirsute pubescence near the base and often with only hirsute pubescence or a limited admixture of glandular trichomes in the inflorescence, very rarely entirely strigulose and glandular-pubescent. Leaves often broader, to narrowly elliptic, the foliage often more bluish green than that of *C. strigulosa*. Flowers often larger, the petals to 5 mm. long and 3.3 mm. wide. Longer filaments to 2.6 mm. long, the shorter to 1.5 mm. long; anthers to 0.8 mm. long. Often more than 30 percent of the pollen with 4 or 5 pores. Style to 5.1 mm. long. Seeds 0.7–0.9 mm. long. Gametic chromosome number, $n=21$. Autogamous.

TYPE: On barren sandy soils of the interior parts of the Columbia River, Washington or Oregon, 1825–6, *D. Douglas* (K; isotype, BM).

DISTRIBUTION (Figure 65): Open or grassy slopes and flats, usually on sandy soil: southern Vancouver Island, British Columbia, and San Juan and Whidbey Islands, northwesternmost Washington; Klickitat and Walla Walla Counties, southern Washington, and Adams and Ada Counties, Idaho, south through east-central Oregon to the vicinity of Reno, western Nevada, and from southwestern Oregon (Douglas, Jackson, and Josephine Counties) south nearly throughout California to the southern San Joaquin Valley and bordering foothills in Kern County; generally away from the coast from Sonoma County, California, southward, where replaced by *C. strigulosa*. From sea level to 7,500 ft. alt.

Vouchers for chromosome number (42 individuals, 40 populations), $n=21$:

U.S.: CALIFORNIA: CONTRA COSTA CO.: Antioch, R18142; ca. 1 mi. S. of Oakley, R18144. FRESNO CO.: 1.6 mi. S. of Easton, R18328· Fresno, R17067; 3.3 mi. N. of Selma, R17065. HUMBOLDT CO.: Near Arcata, R18373; 1 mi. E. of Dinsmores, R18367. KERN CO.: West of mouth of Kern River canyon, *Wedberg & Lewis* 1671 (LA); Miracle Hot Springs, R17567 (progeny = R18773), R18805; Isabella, R18800; 0.5 mi. W. of Weldon, R18798 (sympatric with *C. strigulosa*); Weldon, R18795 (sympatric with *C. strigulosa*); Havilah, R17568; Black Mt. burn, Greenhorn Mts., 3,500 ft., *Howell* 38215 (CAS; progeny = R18785; sympatric with *C. campestris* subsp. *campestris* and *C. strigulosa*). LAKE CO.: 3 mi. S. of Kelseyville, *Breedlove* 5143; 2 mi. NE. of Lower Lake, *Breedlove* 4540; 9.9 mi. N. of Lower Lake, R18240; Lakeport R18239. LASSEN CO.: 4.8 mi. N. of Milford, R17872. MADERA CO.: 7.6 mi. S. of Coarsegold, R18340; 0.7 mi. W. of Oakhurst, R18344. MERCED CO.: Ca. 20 mi. W. of Merced, *Klein* 444 (RSA; progeny, DS). MONTEREY CO.: 1.5 mi. W. of Bradley, R18206: 4.1 mi. N. of Mission San Antonio,

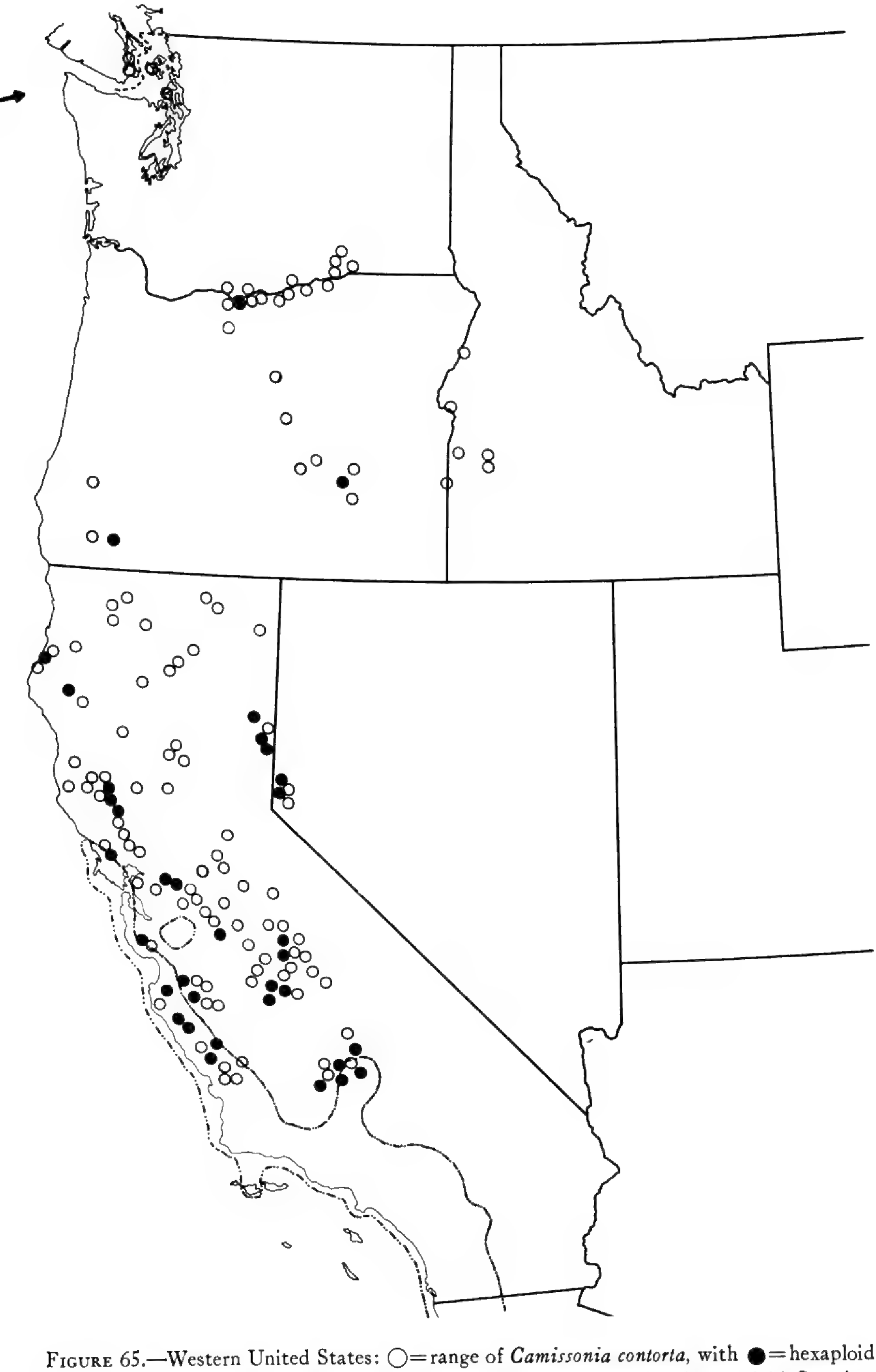


FIGURE 65.—Western United States: ○=range of *Camissonia contorta*, with ●=hexaploid chromosome counts ($n=21$). Northern limits of the closely related tetraploid *C. strigulosa* indicated by dotted line.

Breedlove 2278; 1.6 mi. N. of junction to Jamesburg, Carmel Valley, R18149; Jolon, R18154; 10 mi. N. of Hunter Liggett Military Reservation Headquarters on road to The Indians, R18272. PLUMAS CO.: 3.1 mi. W. of Vinton, R18418; 4.8 mi. W. of Vinton, R18420. SAN BENITO CO.: Panoche Creek Campground, Pinnacles, *Breedlove* 2182; 1.1 mi. S. of Cienaga School, near Hollister, R18199. SAN LUIS OBISPO CO.: 1.8 mi. W. of Bee Rock, R18302, 18303; Atascadero, R18280. SONOMA CO.: 3 mi. S. of Sebastopol, *Breedlove* 3706. TULARE CO.: Posey to White River, R20239; Kern River Canyon 6 mi. S. of Roads End P.O., 3,100 ft., *Howell* 33134 (CAS; progeny = R18770). NEVADA: STOREY CO.: 4.7 mi. N. of Carson City, R18544. WASHOE CO.: Ca. 5 mi. N. of Reno, *Mosquin & Gillett* 5310 (DAO; progeny = R18780). OREGON: HARNEY CO.: 5.3 mi. N. of Narrows, R18455. JACKSON CO.: Just N. of Central Point, R18381. WASCO CO.: 2.2 mi. W. of Sherman Co. line along Columbia R., R18385.

REPRESENTATIVE SPECIMENS EXAMINED:

CANADA: Saanich Spit, *Eastham* in 1942 (NMC, UBC); Cedar Hill, near Victoria, *Macoun* in 1887 (NMC).

U.S.: CALIFORNIA: AMADOR CO.: 2 mi. NNE. of Buena Vista, ca. 300 ft., *Howell* 29808 (CAS). BUTTE CO.: Chico, *Copeland* 3033 (POM); hills 8 mi. N. of Oroville, *Heller* 11330 (CAS, DS, GH, NY, OSC, PH, UC, US, WTU). CALAVERAS CO.: 2 mi. W. of Camanche, 400 ft., *Belshaw* 1978 (UC); Mokelumne Hill, *Blaisdell* (CAS). CONTRA COSTA CO.: Alhambra Valley, *Rattan* in 1887 (DS); Nortonville, *Bacigalupi* 4977 (JEPS). ELDORADO CO.: Coloma, *Reed* in 1941 (UC). FRESNO CO.: Hwy. 180 just below 4,000 ft. marker, *Quibell* 1963 (RSA); Shaver, 5,200 ft., *Hall & Babcock* 292 (UC); Millwood Meadow, near Sequoia Lake, 5,100 ft., *Simonian* 482 (herb. Fresno State College); Clovis, *Thompson* in 1902 (DS, POM). HUMBOLDT CO.: Klamath R. at mouth of Slate Creek, 400 ft., *Tracy* 16244 (UC). KERN CO.: Cedar Canyon just below mouth of Fulton Creek, Greenhorn Range, 3,250 ft., *Twisselmann* 8495 (DS); Walker Basin, 3,400 ft., *Twisselman*, 9518 (CAS, DS, RSA); 16 mi. S. of Bodfish, *Thorne* 31736 (DS, RSA); Poso Creek, *Hall & Babcock* 5012 (DS, GH, PH, UC). LAKE CO.: Dashiels, Mt. Sanhedrin, *Eastwood* in 1925 (CAS); W. base of Snow Mt., *Ackley* in 1965 (CAS); Jordan Park, *Jussel* in 1932 (POM). LASSEN CO.: Milford, *Baker* in 1890 (UC); Chat, 5,000 ft., *Jones* in 1897 (POM). MADERA CO.: N. side of Millerton L., 550 ft., *Bacigalupi* 7672 (JEPS); Bass Lake, 3,300 ft., *Quibell* 2452 (POM); 5 mi. NE. of Madera, *Howell* 41073 (CAS). MARIPOSA CO.: Just S. of Mormon Bar, 1,800 ft., *Howell* 40571 (CAS). MENDOCINO CO.: Sand in the Russian R., Ukiah, *Bolander* 3857 (F, NY); Navarro, *Byxbee* in 1895 (JEPS); near Longvale, 1,500 ft., *Tracy* 9924 (UC, WTU). MERCED CO.: Delhi, *Howell* 35293 (CAS); 2 mi. SW. of Livingston, *Stage* 59–59 (RSA, UC); Merced R. bottom between Snelling and Hopeton, *Howell* 1049 (CAS). MODOC CO.: Parker Creek SE. of Alturas, 5,200 ft., *Payne* 637 (JEPS); sink along highway between Malin and Canby, several miles N. of quarantine station, *Baker* 8309 (POM). MONTEREY CO.: Trail to Ventana Double Cone, 4,000 ft., *Hardham* 10127 (DS); 3 mi. NE. of Pleyto Well, SW. of Bradley, 550 ft., *Graham* 266 (RSA, UC). NAPA CO.: Howell Mt., *Jepson* 14478 (JEPS); Capell Valley, 700 ft., *Kamb & Chisaki* 1761 (UCSB). PLUMAS CO.: Near Beckwourth, 4,880 ft., *Howell* 37800 (CAS). SAN BENITO CO.: 5.4 mi. S. of Willow Creek School on road to the Pinnacles, *Ferris* 8347 (CAS, DS, GH, POM, UC); Panoche Pass, *Abrams & Borthwick* 7984 (DS, NY, POM); 3.7 mi. from Hernandez on road to New Idria, R15088 (DS). SAN JOAQUIN CO.: 8.8 mi. S. of Stockton, R9132 (CAS); Mokelumne, 200 ft., *Roseberry* 160 (UC); Tracy, *Baker* 2775 (CAS, F, GH, NY, POM, RM, UC, US). SAN LUIS OBISPO CO.: Palo Prieto

Canyon, *Ferris* 12816 (DS); Atascadero, *Hardham* 3054 (LA, SBBG). SANTA CLARA CO.: Stanford University, *Elmer* 2368 (NY, US). SANTA CRUZ CO.: Bielawski Look Out Station, 3,270 ft., *Thomas* 1514 (DS, OSC); Deer Ridge Farm, summit of Santa Cruz Mts., 2,800 ft., *Pendleton* 371 (POM, UC). SHASTA CO.: Near McArthur, *Eastwood & Howell* 7955 (CAS, POM); Hat Creek ca. 20 mi. W. of Fall River Mills, *Hitchcock* 6554 (POM, WTU); near Redding, *Heller* 7888 (GH, NY, PH, US). SISKIYOU CO.: French Creek Logging Road W. of Callahan, 3,500–4,000 ft., *Ferris & Lorraine* 11757 (DS, RSA, UC, WTU); Scott Valley, 2,900 ft., *Parker* 406 (NMC, UC); Yreka Creek, Siskiyou Mts., 2,800 ft., *Wheeler* 3527 (POM, RSA, UC); near Yreka, *Greene* in 1876 (F). SONOMA CO.: Pitkin Marsh near Forestville, *Rubtzoff* 1027 (UC). STANISLAUS CO.: 8 mi. E. of Oakdale, *Hoover* 3956 (UC); Turlock, *Fosberg* in 1927 (POM); Modesto, *Hoover* 889 (UC). SUTTER CO.: South Peak, Marysville Buttes, *Jepson* 14478 (JEPS, UC). TEHAMA CO.: 6 mi. W. of Paskenta, *Bailey* in 1938 (JEPS). TRINITY CO.: Three Forks of Mad River, 2,900 ft., *Tracy* 10175 (DS, UC). TULARE CO.: Sand along Tule R., *Dudley* in 1897 (DS); Johnsondale, 4,670 ft., *Howell* 37343 (CAS). TUOLUMNE CO.: Tuolumne R. just below junction of Middle and South Forks, R8234 (CAS). IDAHO: ADA CO.: Boise, 2,880 ft., *Clark* 38 (DS, F, GH, NY, POM, RM, UC, US, WS, WTU). CANYON CO.: New Plymouth, 2,200 ft., *Nelson & Macbride* 777 (RM); Big Willow, 3,000 ft., *Macbride* 158 (GH, NY, RM, US). OWYHEE CO.: Jump Creek Canyon, R13391 (DS). WASHINGTON CO.: Weiser, 2,200 ft., *Jones* in 1900 (POM). NEVADA: STOREY CO.: Carson City, 5,000 ft., *S. Watson* in 1868 (NY). WASHOE CO.: Reno Hot Springs to Steamboat Springs, 5,200 ft., *Train* 3557 (NY, UC). OREGON: CROOK CO.: Hay Creek, 730 mi., *Leiberg* 204 (F, GH, NY, ORE, UC, US, WS). DOUGLAS CO.: Bluffs of the Umpqua R. opposite Roseburg, *Constance & Rollins* 2959 (DS, GH, NMC, NY, RM, RSA, UC, US, WS, WTU). GILLIAM CO.: 6 mi. E. of Arlington, R18390 (UC, WS, WTU). HARNEY CO.: 28 mi. from Burns on road to Lakeview, *Howell* 28697 (CAS); 12 mi. N. of Frenchglen, *Peck* 25262 (OSC, UC). HOOD RIVER CO.: Hood River, *Suksdorf* in 1895 (WS). JACKSON CO.: 2 mi. N. of Central Point, *Peck* 14968 (US). JOSEPHINE CO.: Grants Pass, *Henderson* in 1886 (DS). MORROW CO.: 0.5 mi. E. of Boardman, *Cronquist* 6239 (NY, OSC, RSA, US, WS, WTU). SHERMAN CO.: Mouth of John Day R., *Hitchcock* 20435 (WTU). UMATILLA CO.: Umatilla, *Jones* in 1902 (POM). WASCO CO.: The Dalles, *Sheldon* 10263 (DS, F, GH, NY, POM, US, WS); Tygh Valley, *Flinn* in 1913 (ORE). WHEELER CO.: 2 mi. SW. of the Painted Hills, ca. 10 mi. NW. of Mitchell, 2,300 ft., *Cronquist* 7269 (NY, OSC, RSA, US, WS, WTU). WASHINGTON: BENTON CO.: Collidge, *ZFR* in 1910 (WS). FRANKLIN CO.: Pasco, *Piper* 2965b (WS). ISLAND CO.: Whidbey I., *Gardner* (POM, UC). KLICKITAT CO.: Carley to Roosevelt, *Pickett et al.* 1433 (WS); near Rockland, *Suksdorf* 5098–5101 (DS, F, US, WS). SAN JUAN CO.: Cattle Point, San Juan I., *Peck* 12711 (WS, WTU). WALLA WALLA CO.: Wallula, *Booth* in 1944 (WS).

As mentioned in the discussions of the preceding species of this section, some populations of *Camissonia contorta*, the only hexaploid species of the group, are very difficult to distinguish from those of the tetraploid *C. strigulosa*. *Camissonia contorta* probably arose, at least in part, following hybridization between the diploid *C. campestris* subsp. *campestris* and the tetraploid *C. strigulosa*, but some populations referred to this species may also have originated following the functioning of an unreduced gamete in a tetraploid plant. *Camis-*

sonia contorta has been found growing sympatrically with *C. kernensis* subsp. *kernensis*, *C. pubens*, *C. parvula*, *C. campestris* subsp. *campestris*, *C. campestris* subsp. *obispoensis*, *C. sierrae*, *C. lacustris* (populations in near vicinity), *C. strigulosa*, and *C. integrifolia*. Hybrids have been observed with *C. campestris* subsp. *campestris*, *C. campestris* subsp. *obispoensis*, and *C. strigulosa*, but these were highly sterile, and there is no evidence of intergradation between *C. contorta* and any other species. Whether the northern and southern populations of this hexaploid differ from one another enough to merit formal taxonomic recognition (particularly in view of the large gaps in the range) remains to be seen; I cannot identify any consistent differences between them at present.

Hexaploid populations were referred by Munz (Bot. Gaz. 85: 251–257. 1928) to *Oenothera contorta* var. *typica* (virtually all of this taxon), var. *epilobioides*, and var. *strigulosa* (a few northern populations only; mostly=*C. strigulosa*). In his more recent treatment of the group (N. Amer. Fl. II. 5: 156–157. 1965) he presented a very confusing treatment, recording *Oenothera contorta* var. *contorta* as diploid, which, so far as I am aware, it never is; placing some hexaploid populations with his *Oenothera dentata*, which name I now restrict to South American plants; and recognizing as a species *Oenothera cruciata*, said to have n=7, and consisting of a mixture of late-season plants of *Camissonia campestris* subsp. *campestris* ($n=7$), the Clear Lake, Lake County, California, populations of *C. lacustris* ($n=14$), and some relatively large-flowered plants of *C. contorta* ($n=21$).

Section VII. *Eremothera*

Camissonia sect. *Eremothera* Raven, Brittonia 16: 285. 1964.

Oenothera subg. *Sphaerostigma* sensu Munz, Bot. Gaz. 85: 234. 1928; pro parte.

Oenothera sect. *Eremothera* (Raven) Munz, N. Am. Fl. II. 5: 148. 1965.

Annuals, the plants caulescent, with no well-defined basal rosette, but the leaves sometimes clustered near the base; plants usually with conspicuous exfoliating white rhytidome, often reddish; plants flowering from the base or not. Leaves subsessile or petiolate, sometimes purple-dotted. Inflorescence erect or nodding at anthesis and becoming erect in fruit. Flowers opening near sunset. Ovary lacking a sterile projection. Petals white, only rarely reddish initially but always fading reddish after fertilization, without any dots or markings. Anthers yellow; stigma and inside of hypanthium greenish; filaments and style white. Capsule sessile regularly but sometimes tardily loculicidal, straight or much contorted, often somewhat torulose, the seeds in one row in each locule, the friable central column much distorted by the seeds at maturity. Seeds either of two kinds, those of the body of

the capsule sharply angular, truncate-ellipsoid, dark brown, coarsely papillose, those of the beak narrowly obovoid or narrowly oblanceolate, smooth or finely lacunose, or all of the second type (figs. 71, 72).

TYPE SPECIES: *Camissonia refracta* (S. Wats.) Raven.

DISTRIBUTION: Mainly in the interior deserts and bordering areas, from east-central Washington, central and southern Idaho, and western Wyoming south through western Colorado to trans-Pecos Texas, northern Sonora, northeastern and central Baja California, and the deserts of California, whence north in the inner Coast Ranges to Alameda and San Joaquin Counties; loose, sandy, or clay soil, on brushy or open slopes and flats.

The clearly related species of *Camissonia* sect. *Eremothera* can easily be divided into four distinctive groups: The first consists of the self-incompatible *C. refracta* and its more widely distributed autogamous derivative, *C. chamaenerioides;* second, the polymorphic, self-incompatible *C. boothii*, here divided into six subspecies, and its two autogamous, smaller flowered derivatives, *C. pygmaea* and *C. gouldii;* third, *C. nevadensis*, a localized endemic of clay soil in west-central Nevada which is very likely an outcrosser and may or may not be self-incompatible; and fourth, the highly autogamous, widespread *C. minor*, which does not appear to be closely related to any of the other groups. In contrast to sect. *Holostigma* and sect. *Camissonia*, which contain majorities of polyploid species, sect. *Eremothera* resembles sect. *Chylismia* and sect. *Eulobus* in being almost exclusively diploid, the one exception being one of the two strains of the autogamous *C. pygmaea* that was examined cytologically; this plant was tetraploid ($n=14$). I cannot make any useful suggestions as to whether *C. refracta* or *C. boothii* is more primitive within this group, but it is clear that the autogamous species have all been derived from self-incompatible ancestors. *Camissonia nevadensis* is comparable with *Boisduvalia cleistogama* Curran, an annual species of another tribe of the family (Epilobieae), in inhabiting heavy clay soil and having decumbent branches with tardily dehiscent capsules which shed their seed only following rains and many months after the flowers were open and the plants were green. As pointed out earlier in this paper, *Camissonia graciliflora* and *C. palmeri* also share this unusual habit; I do not know of any comparable species of Onagraceae, although a number of genera in other families that occur in the same places have produced one or more species that are somewhat comparable.

In general, the outcrossing species of *Eremothera* are visited and pollinated by small moths in the evening after they open and sometimes also by bees early the following morning. At a few, widely scattered localities, *Camissonia boothii* subsp. *decorticans* opens its flowers about an hour before sunset and is visited and pollinated by

the large, oligolectic bee *Andrena* (*Onagrandrena*) *vespertina* Linsley & MacSwain. Most populations of this subspecies, and most (if not all) other populations of the section open their flowers at or shortly after sunset, and there is generally not enough time for visitation by bees before darkness.

In his revision of this group, Munz (Bot. Gaz. 85: 233–270. 1928) recognized *C. refracta*, *C. chamaenerioides*, *C. nevadensis*, and *C. minor* with the same limits accepted in the present paper. No problems have arisen subsequently concerning the delimitation of these distinctive species. *Camissonia pygmaea* was considered a variety of *C. boothii*, but I raised it to specific rank in 1964 (Raven, Brittonia 16: 285) because of its nonoverlapping pattern of variation. This entity is autogamous, in contrast to the self-incompatible and much larger flowered *C. boothii;* the separation of these two taxa at the specific rank was subsequently accepted by Munz (N. Amer. Fl. II. 5: 154. 1965). *Camissonia gouldii* is described in the present revision from material that was not available to Munz at the time of his 1928 paper; like *C. pygmaea*, it is evidently an autogamous derivative of *C. boothii.*

The populations here grouped as *C. boothii* were separated by Munz (Bot. Gaz. 85: 233–270. 1928) into three species: *Oenothera decorticans*, with four intergrading varieties; *O. boothii;* and *O. alyssoides*. Three of the four varieties of *O. decorticans* are here regarded as subspecies of *Camissonia boothii;* the fourth, var. *rutila*, is regarded as a series of unrelated populations with relatively small flowers in which the petals are red from the time the flowers first open. Intermediate populations are found joining the three species recognized by Munz in 1928, and this is the reason that I considered them best treated as subspecies in 1964. In his 1965 monograph, Munz followed this treatment, describing an additional subspecies, subsp. *intermedia*, which occurs in central Nevada and adjacent easternmost California and links subsp. *boothii* with subsp. *alyssoides*. Dr. Munz and I thought earlier that an additional subspecies, which he described in 1965 as subsp. *inyoensis*, should be recognized; but I have since come to believe that this entity is best treated as part of subsp. *desertorum* as delineated here. At any rate, we both agree that this complex series of populations is best regarded as a single, polytypic species.

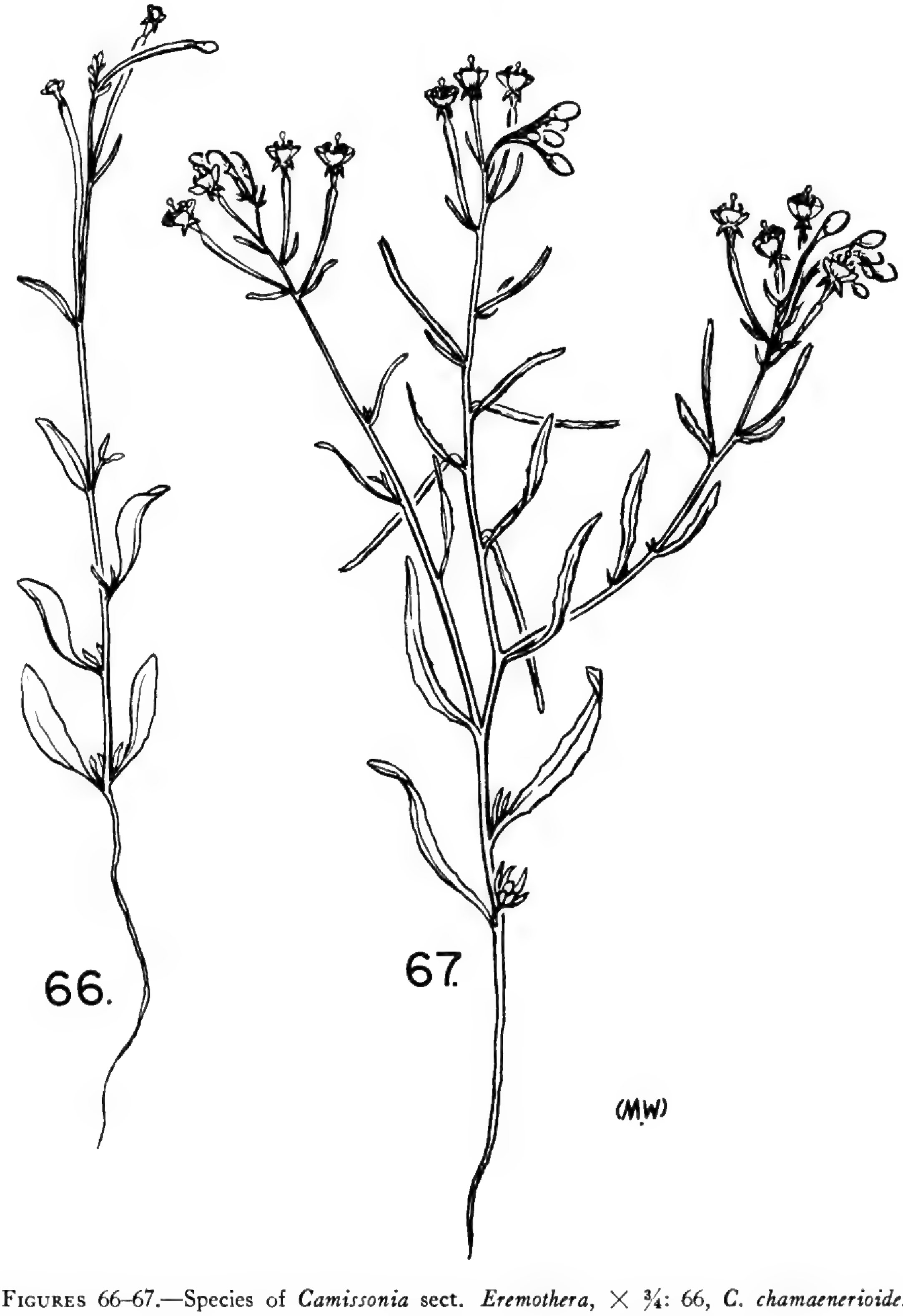
52. Camissonia refracta (S. Wats.) Raven, Brittonia 16: 285. 1964. FIGURE 67

Sphaerostigma refractum (S. Wats.) Small, Bull. Torrey Cl. 23: 192. 1896.

Oenothera deserti M. E. Jones, Contr. West. Bot. 12: 15. 1908. Type: Needles, San Bernardino Co., Calif., 5 May 1884, *M. E. Jones* 3828 (POM: isotypes, DS, GH, US).

Sphaerostigma deserti (Jones) Heller, Muhlenbergia 9: 68. 1913.

Erect, 6–45 cm. tall, often well branched at the base and above, not flowering near the base, sparsely strigulose or with an admixture



FIGURES 66–67.—Species of *Camissonia* sect. *Eremothera*, × ¾: 66, *C. chamaenerioides* (*Gould* 1473, DS); 67, *C. refracta* (*Hitchcock & Muhlick* 22246, DS).

of glandular trichomes in the inflorescence or all over. Leaves very narrowly elliptic to very narrowly lanceolate, the basal ones largest, to 6 cm. long and 0.8 cm. wide, often withered by the time of flowering; leaves sparsely and weakly denticulate; apex acuminate, the base attenuate; basal leaves with a petiole up to 2 cm. long, the

upper ones subsessile. Inflorescence nodding before anthesis. Hypanthium 4–6 mm. long, 1.6–2 mm. across at the summit, villous in lower half within. Sepals 4–6 mm. long, 1.2–2 mm. wide. Petals 3.5–7 mm. long, 2–6 mm. wide. Filaments of the episepalous stamens 2–4.5 mm. long, those of the epipetalous ones slightly shorter; anthers 1.5–2.5 mm. long. Style 9–13 mm. long, the lower portions villous; stigma 1–1.5 mm. in diameter, held well above the anthers at anthesis. Capsule 2–5 cm. long, 0.7–1 mm. thick, straight to contorted, erect, spreading, or reflexed, terete. Seeds all of one type, 0.9–1.5 mm. long, 0.45–0.5 mm. thick, gray, finely lacunose, the lacunae in lines. Gametic chromosome number, $n=7$. Self-incompatible.

LECTOTYPE: Gravelly hills near the Colorado River, Arizona or California, 17 February 1854, *J. Bigelow* (GH); cf. Munz, Bot. Gaz. 85: 237. 1928.

DISTRIBUTION (Figure 68): Sandy desert slopes and flats from southernmost Esmeralda, southern Nye, and Clark Counties, Nevada, and Washington County, southwestern Utah, south throughout the Mojave and Colorado Deserts of Inyo, San Bernardino, Imperial, central and eastern Riverside, and eastern Kern and San Diego Counties, California; Mohave, Yuma, and western Pima Counties, Arizona. A single collection has been seen from Hidalgo County, New Mexico (east of Lordsburg, *Jones* in 1930, POM), but this is from some 250 miles out of the usual range. I have not mapped it and feel that the locality should be reconfirmed by further collections. From about 100 ft. below sea level to 4,500 ft. alt.

Vouchers for chromosome number (15 individuals, 12 populations), $n=7$:

U.S.: ARIZONA: YUMA CO.: Ca. 20 mi. E. of Yuma, *H. & M. Lewis* 1640 (LA; 2 pairs + ring of 10); 20 mi. N. of Yuma, R14837 ($n=7$); 4.3 mi. E. of Ehrenburg, R11597 (2 plants, both with 5 pairs + ring of 4). CALIFORNIA: IMPERIAL CO.: 23 mi. N. of Ogilby, *Klein* 119 (7 pairs). INYO CO.: Sheppard Canyon, Panamint Valley, *T. & L. Mosquin* 4312 (4 pairs + ring of 6); Harrisburg Flats, Panamint Mts., *Gregory* 399 (RSA; 5 pairs + ring of 4). RIVERSIDE CO.: Box Canyon, *Lewis* 1623 (LA; 5 pairs + ring of 4), 1633 (LA; 3 pairs + 2 rings of 4); Corn Springs, Chuckwalla Mts., R11577 (2 plants, both with 5 pairs + ring of 4); Fargo Canyon, R11439 (2 plants, both with 7 pairs). SAN BERNARDINO CO.: Near Whipple Mts., *Klein* 1394 (7 pairs). NEVADA: CLARK CO.: Ranger Mts., R18916 ($n=7$).

Camissonia refracta is distinctive and has rarely been confused with any other entity. It often grows sympatrically with *C. chamaenerioides*, *C. boothii* subsp. *condensata*, and *C. boothii* subsp. *desertorum*, but no hybrids have been observed in nature. The high degree of chromosomal heterozygosity in this species is striking and could well be investigated further; of the 13 individuals in which chromosome association has been observed, 4 had 7 pairs; 6 had 5 pairs and a ring of 4; 1 had 3 pairs and 2 rings of 4; 1 had 4 pairs and a ring of 6;

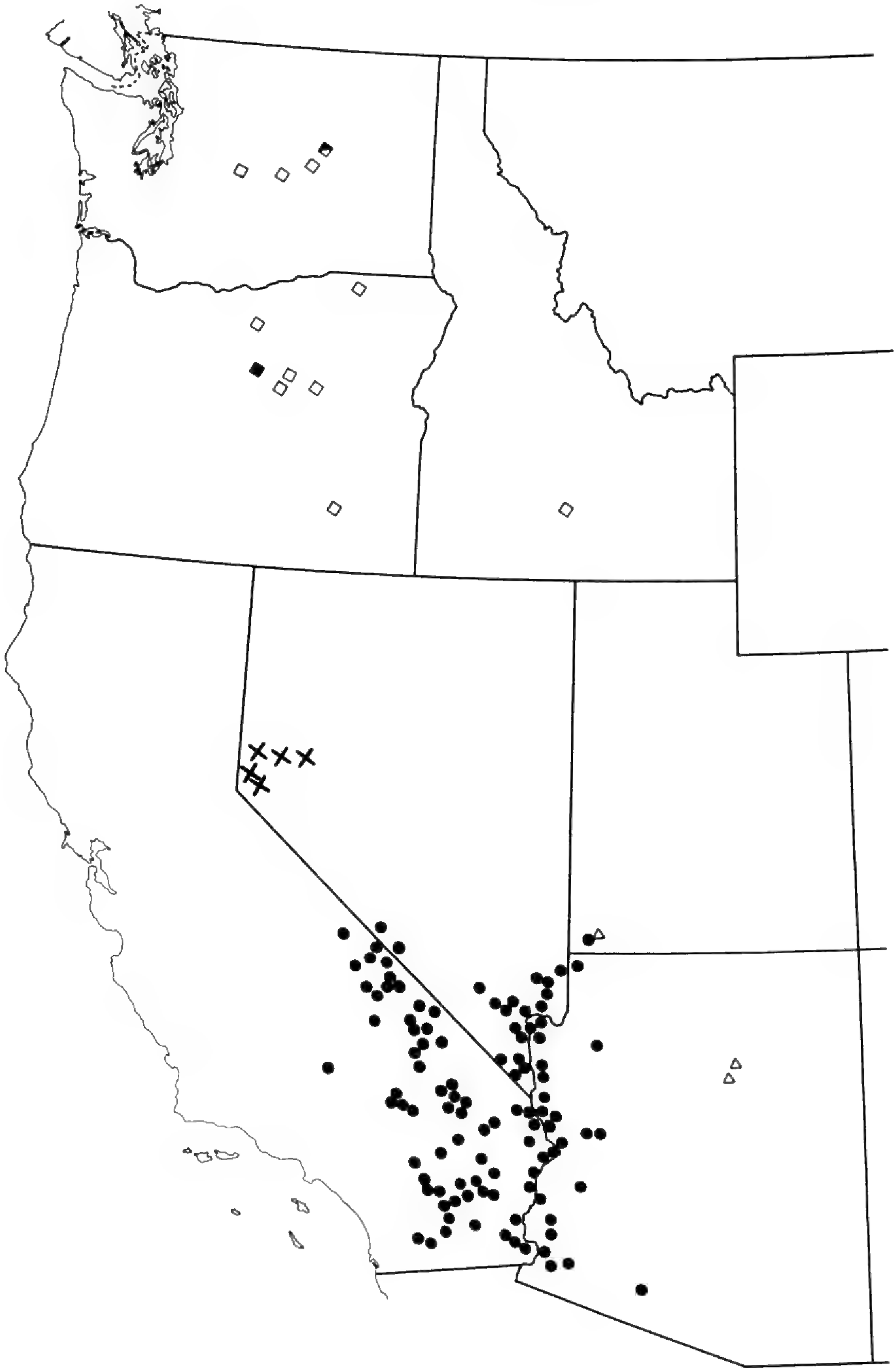


FIGURE 68.—Western United States, showing the ranges of species of *Camissonia* sect. *Eremothera:* ●=*C. refracta;* ×=*C. nevadensis;* ◇=*C. pygmaea,* with ◆=diploid chromosome count ($n=7$) and ◈=tetraploid count ($n=14$); △=C. gouldii.

and 1 had 2 pairs and a ring of 10. There is no evidence that any of these configurations is associated with balanced lethals as in certain species of *Oenothera*, *Gayophytum*, *Calylophus*, and *Gaura;* but it would seem on the basis of our present limited amount of evidence that well over half of the individuals of this species are heterozygous for at least one reciprocal translocation, a situation unknown elsewhere in *Camissonia*. Six individuals from the Nevada population cited above were found to be self-incompatible by pollen-tube growth.

53. Camissonia chamaenerioides (A. Gray) Raven, Brittonia 16: 285. 1964.

FIGURE 66

Sphaerostigma chamaenerioides (A. Gray) Small, Bull. Torrey Cl. 23: 189. 1896.

Sphaerostigma erythrum A. Davids., Bull. S. Calif. Acad. Sci. 1: 118, *pl. 9.* 1902. Type: Dry hill slopes, south of Clifton, Greenlee Co., Ariz., 10 April 1899, *A. Davidson* 244 (LAM; isotypes, DS, UC).

Oenothera erythra (A. Davids.) Macbride, Contr. Gray Herb. 65: 41. 1922.

Erect, 8–50 cm. tall, usually branched near the base, not flowering near the base, glandular-pubescent with an admixture of strigulose pubescence in and near the inflorescence. Leaves very narrowly elliptic, more rarely narrowly elliptic, the basal ones largest, to 8 cm. long and 2.5 cm. wide; leaves entire to very sparsely denticulate; apex acute or acuminate, the base attenuate; petioles of basal leaves 1–3.5 cm. long, the upper leaves subsessile. Inflorescence nodding before anthesis. Hypanthium 1.6–2.3 mm. long, 0.9–1.4 mm. across at the summit, pubescent in lower half within. Sepals 1.5–2.5 mm. long, 0.7–1.3 mm. wide. Petals 1.8–3 mm. long, 1–1.8 mm. wide. Filaments of the episepalous stamens 0.7–1.5 mm. long, those of the epipetalous ones very slightly shorter; anthers 0.5–1.1 mm. long. Style 2.3–4.5 mm. long, the lower portions pubescent; stigma 0.7–1 mm. in diameter, surrounded by the anthers at anthesis. Capsule 3.5–5.5 cm. long, 0.8–0.9 mm. thick, spreading, terete. Seeds similar to those of *C. refracta*, 0.9–1 mm. long, ca. 0.3 mm. thick. Gametic chromosome number, $n = 7$. Autogamous.

TYPE: El Paso, El Paso County, Texas, 1852, *C. Wright* 1377 (GH; isotypes, BM, K, PH, US).

DISTRIBUTION (Figure 50): Sandy desert slopes and flats from northern Inyo County, California, Nye and Lincoln Counties, Nevada, and Washington County, Utah (also known from Dugway, Tooele County, *Jones* 1891, POM), south to the vicinity of Bahía de los Angeles in northeastern Baja California, in Sonora to the vicinity of Luja midway between Hermosillo and Guaymas, throughout Arizona except for the northeastern corner, rare in New Mexico (Dona Ana and Luna Counties), and in trans-Pecos Texas east to Brewster County; also known from Isla Angel de la Guarda in the Gulf of California. Not known from, but to be expected in, Chihuahua. From about 150 ft. below sea level to 4,600 ft. alt.

Vouchers for chromosome number (10 individuals, 5 populations), $n = 7$:

U.S.: ARIZONA: PIMA CO.: 3 mi. N. of headquarters, Organ Pipe National Monument, *H. & M. Lewis* 1639 (3 plants; LA). YUMA CO.: 4.3 mi. E. of Ehrenburg, R11596 (DS); 1 mi. S. of Ehrenburg, R11593 (DS). CALIFORNIA: RIVERSIDE CO.: Corn Springs, Chuckawalla Mts., *Mosquin* 3209 (4 plants; DAO).
BAJA CALIFORNIA: Bahia de los Angeles, *Moran* 12422.

Camissonia chamaenerioides is distinctive and has rarely been confused with any other species. It is similar to *C. refracta* and probably derived from populations relatively similar to that species, but differs not only in flower size but also in leaf shape, pubescence, and seed size. *Camissonia chamaenerioides* is the only species of the genus that occurs in Texas. This species occurs sympatrically with *C. refracta*, *C. boothii* subsp. *condensata*, and *C. boothii* subsp. *desertorum;* no natural hybrids have been observed.

54. Camissonia boothii (Dougl.) Raven, Brittonia 16: 285. 1964.

Erect, 12–65 cm. tall, often well branched at the base and above, usually not flowering near the base, subglabrous, strigulose, villous, or glandular-pubescent. Leaves very narrowly elliptic to narrowly ovate, the basal ones largest, 2–10 cm. long, 0.5–3.8 cm. wide, often withered by time of flowering, sparsely denticulate, the apex acuminate or acute, the base narrowly cuneate to attenuate; basal leaves with a petiole 0.4–6 cm. long, the upper ones subsessile. Inflorescence nodding before anthesis. Hypanthium 4–7 (–8) mm. long, 1.7–2.5 mm. across at the summit, villous in lower half within. Sepals (2.7–) 4–8 mm. long, 1.4–2.3 mm. wide. Petals (3–) 4–7.5 mm. long, (1.75–) 2.6–7 mm. wide. Filaments of episepalous stamens (1.5–) 2–5.8 mm. long, those of the epipetalous ones slightly shorter; anthers (1–) 1.8–2.3 mm. long. Style (6.5–) 8.2–13.5 (–15) mm. long, villous near the base; stigma 1.2–2 mm. across, depressed-globose, held well above the anthers at anthesis. Capsule slightly curved outward to contorted, 0.8–3.5 cm. long, 1–3.8 mm. thick at the base, terete, held on the dried plant and shedding seeds tardily. Seeds all of one type or of two types, the relatively smooth kind (which may be the only kind) 1.4–2.1 mm. long, 0.5–0.7 mm. thick, more or less triangular in transection, light brown, those of the body 0.5–0.9 mm. thick, dark brown, coarsely papillose. Gametic chromosome number, $n = 7$. Self-incompatible.

DISTRIBUTION (Figure 69): Deserty, often brushy or open slopes and flats, from Klickitat, Adams, and Whitman Counties, eastern Washington, and southwestern Idaho, south to eastern California (whence north in the inner Coast Ranges to Alameda and San Joaquin counties), northeastern Baja California, northwestern Sonora, and through western Utah to western Arizona, south to Pima and Pinal Counties. From about 200 ft. below sea level to 6,600 ft. alt.

As explained in the introductory remarks for the section, *Camissonia boothii* is here treated as a polytypic species with six subspecies that replace one another geographically. The seeds are apparently always monomorphic in subsp. *alyssoides* but very rarely so in populations of the other subspecies.

Of the 21 individuals of this species for which meiotic chromosome association was observed, 2 had a ring of 4 chromosomes and 5 pairs, 1 had a ring of 6 and 4 pairs, and 18 had 7 pairs. This suggests the presence of translocation heterozygosity of about the same order of magnitude (about 20 percent) as found in sect. *Chylismia*, but much less than characteristic of *C. refracta*.

54a. Camissonia boothii subsp. **decorticans** (Hook. & Arn.) Raven, Brittonia 16: 285. 1964.

Gaura decorticans Hook. & Arn., Bot. Beechey Voy. 343. 1838.
Oenothera gauraeflora Torr. & Gray, Fl. N. Amer. 1: 510. 1840.
Sphaerostigma gauraeflorum (Torr. & Gray) Walp., Rep. 2: 78. 1843.
Oenothera decorticans (Hook. & Arn.) Greene, Fl. Francisc. 217. 1891.
Oenothera rutila A. Davids., Erythea 2: 62. 1894. Type: Big Rock Creek, San Gabriel Mts., Los Angeles Co., Calif., 8 July 1894, *A. Davidson* (LAM).
Sphaerostigma decorticans (Hook. & Arn.) Small, Bull. Torrey Cl. 23: 191. 1896.
Sphaerostigma rutilum (A. Davids.) Parish, Erythea 6: 89. 1898.
Oenothera alyssoides var. *decorticans* (Hook. & Arn.) Jeps., Man. Fl. Pl. Calif. 686. 1925.
Oenothera decorticans var. *typica* Munz, Bot. Gaz. 85: 245. 1928.
Oenothera decorticans var. *rutila* (A. Davids.) Munz, Bot. Gaz. 85: 245. 1928.
Oenothera boothii subsp. *decorticans* (Hook. & Arn.) Munz, N. Amer. Fl. II. 5: 152. 1965
Oenothera boothii subsp. *rutila* (A. Davids.) Munz, Fl. N. Amer. II. 5: 153. 1965.

Stems 12–65 mm. long, hollow, with conspicuous, exfoliating white or somewhat pinkish or brownish rhytidome. Plants subglabrous, with strigulose or glandular trichomes in the inflorescence. Capsule nearly straight, curved outward, swollen at base, 1.7–2.3 mm. thick near the base, rapidly tapering upward. Seeds dimorphic, 1.4–2.1 mm. long, 0.5–0.7 mm. (smooth type) or 0.8 mm. (papillose type) thick. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: California, 1833, *D. Douglas* (K; isotypes, BM, GH, NY).

DISTRIBUTION (Figure 69): Open, usually steep slopes, often on shale or other loose rocky substrates, endemic to California: inner south Coast Ranges from Alameda and southwestern San Joaquin Counties south to Santa Barbara and Ventura Counties and the San Gabriel Mountains and easternmost Santa Monica Mountains of Los Angeles County, whence north through the Tehachapi Mountains to the western slopes of the southern Sierra Nevada in Kern and southernmost Tulare Counties; from near sea level to 6,000 ft. alt.

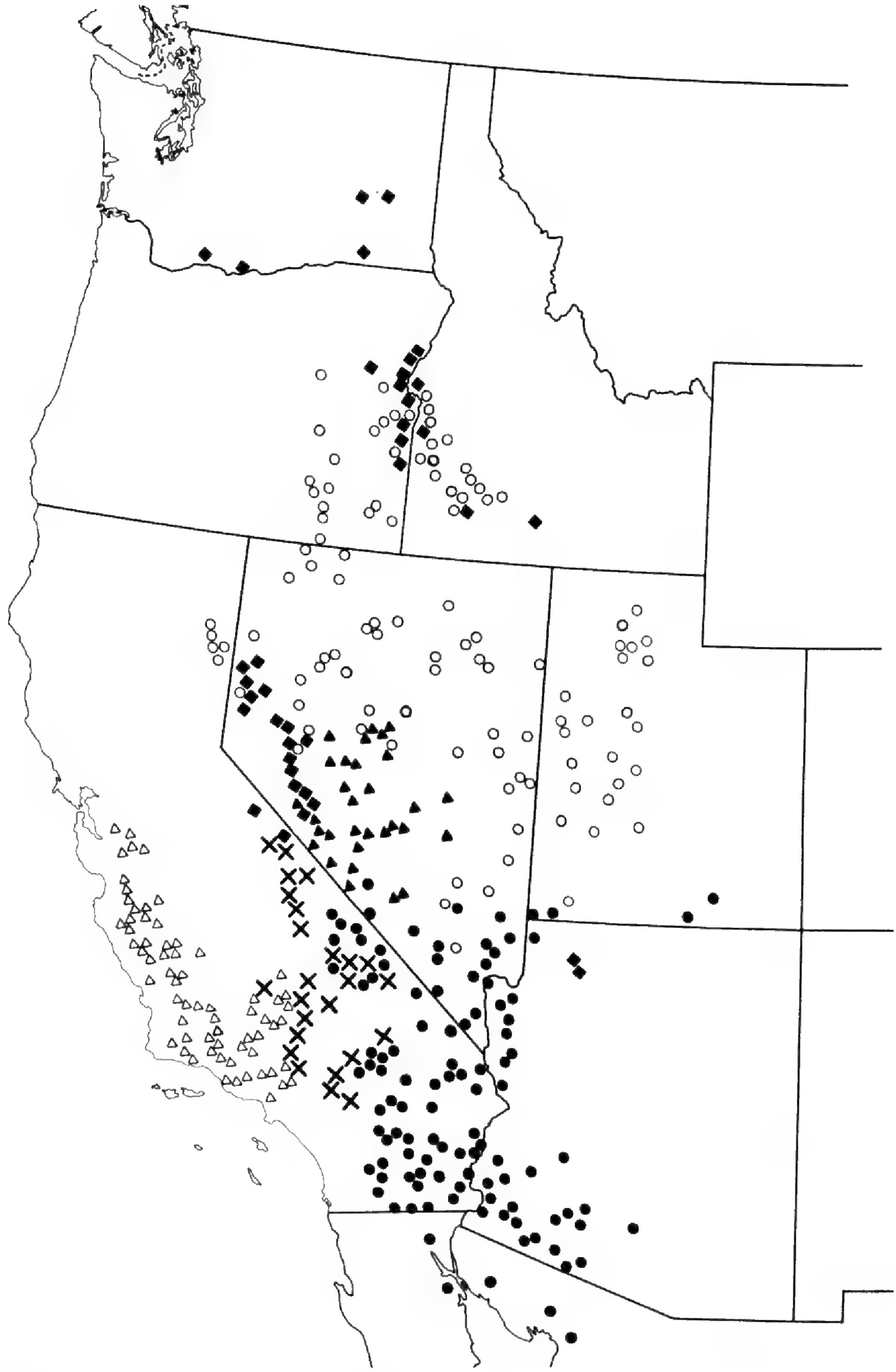


FIGURE 69.—Western United States and a portion of northwestern Mexico, showing the range of *Camissonia boothii:* △=*C. boothii* subsp. *decorticans;* ×=subsp. *desertorum;* ●=subsp. *condensata;* ▲=subsp. *intermedia;* ○=subsp. *alyssoides;* =◆subsp. *boothii*.

Vouchers for chromosome number (19 populations, 10 individuals), $n=7$ (7 pairs in plants marked with an asterisk):

U.S.: CALIFORNIA: KERN CO.: Grocer Grade 5 mi. W. of Maricopa, 2,000 ft., *Breedlove* 2395*; near Havilah, *Lewis* 1106 (2 plants, 1*; LA, RSA, UC). MONTEREY CO.: 4.9 mi. E. of King City, *Breedlove* 2175*. SAN LUIS OBISPO CO.: Carrizo Plain at S. end of Soda Lake, *Bates* 2407; 8.6 mi. W. of Simmler, *Breedlove* 2062; N. road to Adelaida near junction to Nacimiento Dam, R18326; Paso Robles, *Lewis & Thompson* 1101* (LA). SANTA BARBARA CO.: 4.3 mi. W. of Pendola Flats Guard Station, upper Santa Ynez R., 1,600 ft., *Breedlove* 2241. STANISLAUS CO.: Arroyo del Puerto, *Breedlove* 5579.

Camissonia boothii subsp. *decorticans* is the only member of sect. *Eremothera* to occur off the deserts, but it still occurs in related, highly xeric communities. Twenty plants of R18326, cited above, were tested for pollen-tube growth following self- and cross-pollination and found to be self-incompatible, as have four from east San Luis Obispo County, California, *Kyhos* 65–173. This subspecies has not been found growing sympatrically with any other member of the section, but it intergrades with subsp. *desertorum* at the margins of its range. It is usually found away from the coast, but has been found on the bluffs at Taylor Ranch, 1.5 miles east of the mouth of the Ventura River, *Pollard* in 1963 (CAS, SBBG).

Occasional populations of this subspecies at relatively high elevations in the southern part of its range have somewhat smaller flowers and reddish petals; they have been distinguished as *Oenothera rutila* or, more recently, *Oenothera boothii* subsp. *rutila*. In my opinion, there is no evidence that the various populations with this combination of characteristics had a common origin, and, even if they did, they do not appear to constitute a major geographical race comparable with the other subspecies recognized here.

54b. Camissonia boothii subsp. **desertorum** (Munz) Raven, Brittonia 16: 285. 1964.

Oenothera decorticans var. *desertorum* Munz, Bot. Gaz. 85: 246. 1928.

Oenothera boothii subsp. *desertorum* (Munz) Munz, Fl. N. Amer. II. 5: 153. 1965.

Oenothera boothii subsp. *inyoensis* Munz, Fl. N. Amer. II. 5: 153. 1965. Type: Willow Creek, Saline Valley, 800 m, Inyo Co., Calif., 25 April 1942, *A. M. Alexander & L. Kellogg* 2702 (RSA, 41213).

Similar to subsp. *decorticans* but shorter, usually less than 35 cm. tall. Capsule flexuous-contorted, the beak often directed downward, 1–1.6 mm. thick near the base. Gametic chromosome number, $n=7$.

TYPE: 10 miles southwest of Garlic Springs, San Bernardino County, California, 8 April 1924, *P. A. Munz & D. D. Keck* 7881 (POM 48926).

DISTRIBUTION (Figure 69): Desert slopes and washes, endemic to California: from vicinity of Benton Station, Mono County, south in the deserts and east slope of the Sierra Nevada to eastern Kern,

northern Los Angeles, and western San Bernardino Counties; also in the upper Kern River drainage, west to the vicinity of Kernville, and in southeasternmost Tulare County. From 1,500–6,500 ft. alt.

Vouchers for chromosome number (5 individuals, 5 populations), $n=7$:

U.S.: CALIFORNIA: INYO CO.: 3 mi. N. of Big Pine, R14258; road to Westgard Pass, *Lewis* 1085 (LA, RSA, UC; 7 pairs); Marble Canyon, Inyo Mts., R17551 (7 pairs). KERN CO.: Road from Randsburg to Red Rock Canyon, *Wedberg* in 1957 (LA; 5 pairs+ring of 4). MONO CO.: Sherwin Grade, 5,000 ft., *Lewis* 1673 (LA).

As here conceived, *Camissonia boothii* subsp. *desertorum* occupies a position intermediate between subsp. *decorticans* and subsp. *condensata*, both geographically and morphologically. Populations of subsp. *desertorum* from the northern portion of its range are in general more pubescent than those from farther south and were referred by Munz (Bot. Gaz. 85: 241–247. 1929; N. Amer. Fl. II. 5: 151–154. 1965) to subsp. *alyssoides*. They may represent intermediates with that taxon, but do not agree with it in habit, being much more lax, and have much more appressed pubescence. In my view, the only populations of subsp. *alyssoides* in California are those in eastern Lassen County, and the nearest populations to those of subsp. *desertorum* are in the Sheep Range of northern Clark County, Nevada, and in Churchill County, Nevada. I have also included in subsp. *desertorum* those populations from the Panamint Mountains Inyo, County, California, listed by Munz (Bot. Gaz. 85: 245. 1929) as approaching *Oenothera decorticans* var. *rutila;* these were apparently also included in subsp. *desertorum* by Munz in his more recent work on the group (N. Amer. Fl. II. 5: 153–154. 1965).

Populations from the eastern slope of the Inyo Mountains and elsewhere in Inyo County, California, where they grow on limestone, have relatively small flowers and lax inflorescences, which make them appear quite distinct in appearance. They were named *Oenothera boothii* subsp. *inyoensis* by Munz in 1965, and at the time, I too thought that they deserved formal taxonomic recognition. Intergradation with other populations more typical of subsp. *desertorum* is so broad and complete that it is often impossible to assign particular plants to one or the other with confidence. Therefore I now consider that they are best assigned to subsp. *desertorum*, despite the fact that their inclusion makes subsp. *desertorum* quite heterogeneous.

A few collections made within the range of subsp. *condensata* on the western Colorado Desert of California appear to be this subspecies; for example, *Parish* in 1882 (JEPS) from Whitewater, Riverside County. These may be extreme variants of subsp. *condensata* or may represent relict populations of subsp. *desertorum* in an area now largely occupied by subsp. *condensata*, which may be of relatively recent derivation.

54c. Camissonia boothii subsp. **condensata** (Munz) Raven, Brittonia 16: 285. 1965.

Oenothera decorticans var. *condensata* Munz, Bot. Gaz. 85: 247. 1928.

Oenothera boothii subsp. *condensata* (Munz) Munz, N. Amer. Fl. II. 5: 154. 1965.

Similar to subsp. *desertorum*, but shorter, 5–20 (–30) cm. tall, the stems very thick, the inflorescence more crowded. Capsules 2–3.8 mm. thick near the base, more or less quadrangular, tapering abruptly, the midribs of the valves very prominent, yellowish. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: Dos Palmos Spring, Riverside County, California, 31 January 1926, *P. A. Munz* 9960 (POM 98708).

DISTRIBUTION (Figure 69): Desert slopes and washes, in sandy soil, from the vicinity of Death Valley, Inyo County, California, south to the region around Barstow, San Bernardino County, and throughout the Colorado Desert of Riverside, Imperial, and eastern San Diego Counties, to the region about the head of the Gulf of California in Baja California and Sonora (south to about 31°30′ N. lat.); eastward to Esmeralda, southern Nye and Lincoln, and Clark Counties, Nevada, and Washington County, Utah, and western Mohave, Yuma, Maricopa, southwesternmost Pinal, and westernmost Pima Counties, Arizona; also in Glen Canyon, San Juan County, Utah (*Gaines* 927, 1011, WS). From about 250 ft. below sea level to 4,000 ft. alt.

Vouchers for chromosome number (8 individuals, 7 populations), $n=7$:

U.S.: ARIZONA: MARICOPA CO.: Near Sentinel, R14826. MOHAVE CO.: 48 mi. NW. of Kingman, *Munz et al.* 22985 (5 pairs + ring of 4). CALIFORNIA: IMPERIAL CO.: Coyote Wells, *Breedlove* 1847; 1 mi. N. of U.S. Hwy. 80 on road to Ogilby, *Klein* 94 (2 plants, 7 pairs). RIVERSIDE CO.; Box Canyon, *Lewis* 1663 (LA; 7 pairs). SAN DIEGO CO.: Borrego Valley, *Lewis* 1624 (LA; 7 pairs), *Wedberg* in 1957 (LA).

As noted by Munz in the protologue of this taxon (Bot. Gaz. 85: 247. 1928), it is very distinctive in fruit, the plants persisting in a dried condition for a long time and shedding their seeds tardily. *Camissonia boothii* subsp. *condensata* intergrades broadly with subsp. *desertorum* where their ranges approach one another. Twelve plants from Frenchman Flat, Nye County, Nevada (R18853), were found to be self-incompatible by pollen-tube growth following cross- and self-pollination.

54d. Camissonia boothii subsp. **alyssoides** (Hook. & Arn.) Raven, Brittonia 16: 285. 1964.

Oenothera alyssoides Hook. & Arn., Bot. Beechey Voy. 340. 1838.

Holostigma alyssoides (Hook. & Arn.) Hook., Icon. 4: 339. 1840.

Sphaerostigma alyssoides (Hook. & Arn.) Walp., Rep. 2: 78. 1843.

Oenothera alyssoides var. *villosa* S. Wats., Proc. Amer. Acad. 8: 591. 1873. Type: Near Salt Lake, Utah, *Capt. H. Stansbury* (GH; isotype, NY).

Sphaerostigma utahense Small, Bull. Torrey Cl. 23: 191. 1896. Lectotype: Milford, Beaver Co., Utah, June 1880, *M. E. Jones* (NY).
Sphaerostigma alyssoides var. *macrophyllum* Small, Bull. Torrey Cl. 23: 192. 1896; nom. subs.
Oenothera gauraeflora var. *hitchcockii* H. Lév., Monogr. Onoth. 226. 1905. Type: Simpson's Park, Utah, 6 July 1859, collector not known (MO).
Sphaerostigma hitchcockii (H. Lév.) A. Nels., Bot. Gaz. 40: 226. 1905.
Oenothera utahensis (Small) Garrett, Spring Fl. Wasatch Reg. 64. 1911.
Sphaerostigma implexum A. Nels., Bot. Gaz. 52: 267. 1911. Type: Falk's Store, 2,200 ft., Canyon Co., Idaho, 17 May 1910, *J. F. Macbride* 27 (RM; isotypes, GH, UC, US, WS, WTU).
Sphaerostigma macrophyllum Rydb., Bull. Torrey Cl. 40: 66. 1913.
Oenothera alyssoides var. *typica* Munz, Bot. Gaz. 85: 242. 1928.
Oenothera boothii subsp. *alyssoides* (Hook. & Arn.) Munz, N. Amer. Fl. II. 5: 154. 1965.

Similar to subsp. *desertorum*, the plants 3–35 cm. tall, sometimes flowering near the base, with leafier stems and a less prominent basal rosette, the leaves relatively small. Plants strigulose, often densely so, especially in the inflorescence, or more rarely villous or with an admixture of glandular trichomes. Capsule 1–1.4 mm. thick, usually very contorted and crowded. Seeds monomorphic, smooth. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: Pine Creek, Snake River plains, southern Idaho, probably in July 1830, *D. Douglas* (K; isotype, GH).

DISTRIBUTION (Figure 69): Sandy slopes and flats, often with *Artemisia tridentata*, from Grant and northern Malheur Counties, eastern Oregon and Payette, Ada, and Elmore Counties, southwestern Idaho, south to eastern Lassen County, California, and Churchill, northernmost Nye, Lincoln, and northern Clark Counties, Nevada, and throughout western Utah, south to Piute and Washington Counties. From 2,000 to 5,500 ft. alt.

Vouchers for chromosome number (8 individuals, 8 populations), $n=7$ (7 pairs in those collections marked with an asterisk):

U.S.: CALIFORNIA: LASSEN CO.: 19 mi. S. of Ravendale, R13273. NEVADA: CHURCHILL CO.: 28.9 mi. SW. of Lovelock, *Kyhos* 65–253.* EUREKA CO.: 2.9 mi. W. of Carlin, R18535*. HUMBOLDT CO.: 3.5 mi. W. of Golconda Summit, R18537*. LINCOLN CO.: E. of Panaca, R11255 (CAS, LA, RSA). PERSHING CO.: 20 mi. NE. of Lovelock, R18540. OREGON: LAKE CO.: 3.4 mi. E. of Headquarters, Hart Mt. Antelope Refuge, R13347*. UTAH: MILLARD CO.: 62 mi. SW. of Delta, *Mathias* 3025* (COLO, LA, RSA, UC).

The number of synonyms listed with this taxon attests to its wide range rather than to any extraordinary degree of variability. Self-incompatibility was demonstrated by pollen-tube growth in 21 plants from the locality of R18540, cited above, and three from 28.9 miles southwest of Lovelock, Churchill County, Nevada, *Kyhos* 65–253. *Camissonia boothii* subsp. *alyssoides* intergrades broadly with subsp. *intermedia* and is very similar to subsp. *desertorum*. Certain populations

cited by Munz (Bot. Gaz. 85: 241–244. 1928) are here regarded as belonging to *C. boothii* subsp. *desertorum*, as noted in the treatment of that subspecies.

In general, the last three subspecies of this species consist of plants that persist and flower over a much longer season than the first three, which flower chiefly following the winter rains.

54e. Camissonia boothii subsp. **intermedia** (Munz) Raven, comb. nov.

Oenothera alyssoides var. *villosa* sensu Munz, Bot. Gaz. 85: 243. 1928: pro parte.

Oenothera boothii var. *typica* sensu Munz, Bot. Gaz. 85: 248. 1928: pro parte.

Oenothera boothii subsp. *intermedia* Munz, Fl. N. Amer. II. 5: 152. 1965.

Similar to subsp. *alyssoides*, but densely villous with a dense admixture of glandular trichomes in the inflorescence, the plants usually 5–20 cm. tall, the leaves mostly less than 2.5 cm. long. Seeds dimorphic. Gametic chromosome number, $n=7$.

TYPE: Dry sandy gravel wash, 4 miles south of Cloverdale Ranch on Reese River to Tonopah road, Nye County, Nevada, 16 September 1939, *P. Train* 3455 (RSA 56046; isotypes, UC, WTU).

DISTRIBUTION (Figure 69): Sandy washes and flats, often with *Artemisia tridentata*, in Nevada from southeastern Churchill and southern Lander Counties south throughout Nye and Esmeralda Counties and in southern Mineral County, and in northeastern Inyo County, California; also in the Kingston Range, northeastern San Bernardino County, California. From 5,000–7,000 ft. alt.

Vouchers for chromosome number (2 individuals, 2 populations), $n=7$ (7 pairs observed in 1 plant of population marked with asterisk):

U.S.: CALIFORNIA: INYO CO.: Ca. 4 mi. S. of Oasis, Fish Lake Valley, *Klein* 353 (RSA). NEVADA: NYE CO.: 10 mi. W. of Lockes, *Thompson & Mathias* 1692* (ARIZ, LA, RSA, UC, WTU).

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: INYO CO.: Deep Springs Valley, *Ferris* 1357 (DS): 2 mi. NE. of Willow Spring, Last Chance Mts., 6,000 ft., *Roos* 6396 (DS, RM, RSA, UC). SAN BERNARDINO CO.: Kingston Mts., 0.1 mi. E. of summit of grade between Horse (Thief) and Beck Springs, ca. 5,000 ft., *Wolf* 10515 (RSA). NEVADA: CHURCHILL CO.: 2 mi. E. of Frenchman, *Mills & Beach* C–20 (UC): vicinity of East Gate, 5,100 ft., *Allen* 349 (DS, NY, POM). ESMERALDA CO.: 3 mi. W. of Lida, Silver Peak Range, *Maguire & Holmgren* 25625 (GH, NY, UC, US, WTU); Montezuma Mt. W. of Goldfield, 2,000 m, *Tidestrom* 9764 (GH, US): Icehouse Canyon, W. slope of Silver Peak Range, 5,300 ft., *Alexandria & Kellogg* 5682 (DS, RM, UC, US, WTU); wash leading to summit between Fish Lake Valley and Basalt, *Ferris* 6681 (DS, POM). LANDER CO.: Austin to Big Creek, 6,000 ft., *Kennedy* 4507 (CAS, DS, GH, PH, RM); Austin, 6,000 ft., *Hitchcock & Martin* 5626 (DS, NY, POM, UC, WS, WTU); 18.5 mi. E. of Austin, *Goodner & Henning* 836 (DAO, F, POM, UC). NYE CO.: Warm Springs Valley, *Maguire & Holmgren* 25458 (GH, NY, UC, WTU); Smoky Valley, *Maguire & Holmgren* 25365 (ARIZ, DS, GH, NMC, NY, OSC, UC, US, WS, WTU); 2 mi. NW. of Penelas Mill, 15 mi. NW. of Ione, *Beach* 865 (ARIZ, DS, IDS, NMC, NY, POM, RM, UC, US, WS,

WTU); pass over Pancake Mts., 84 mi. SW. of Ely, 6,000 ft., *Rollins & Chambers* 2497 (DS, GH, RM, UC, US); foothills of Pahute Mesa, N. Forty Mile Drainage, 6,000 ft., *Beatley* 1694 (DS). MINERAL CO.: 10 mi. N. of Basalt, *Tidestrom* 10040 (GH); Candelaria, 6,000 ft., *Shockley* 324 (DS, UC).

This entity bridges the morphological and geographical gap between subsp. *boothii* and subsp. *alyssoides* in Nevada completely. Nevertheless, it consists of a large number of morphologically relatively uniform populations that occupy a sizable range in central Nevada.

54f. Camissonia boothii subsp. **boothii**

Oenothera boothii Dougl., *in* Hook., Fl. Bor. Amer. 1: 213. 1834.

Sphaerostigma boothii (Dougl.) Walp., Rep. 2: 77. 1843.

Oenothera gauraeflora race *boothii* (Dougl.) H. Lév., Monogr. Onoth. 226. 1905.

Sphaerostigma senex A. Nels., Proc. Biol. Soc. Wash. 18: 173. 29 June 1905. Type: Pyramid Lake, Washoe Co., Nev., 9 June 1903, *G. H. True* 750 (RM).

Sphaerostigma lemmoni A. Nels., Bot. Gaz. 40: 61. 1905. Type: "East flank of the Sierra Nevada," presumably in Nevada, 1875, *J. G. Lemmon* 103 (MO; probable isotype, US).

Oenothera boothii var. *typica* Munz, Bot. Gaz. 85: 248. 1928.

Oenothera boothii subsp. *boothii* Munz, N. Amer. Fl. II. 5: 151. 1965.

Similar to subsp. *intermedia*, but often more robust, and the leaves broader, lanceolate or narrowly ovate, the cauline ones especially proportionately broader, 0.8–6 cm. long, 0.6–2.2 mm. broad, more coarsely serrulate, the plants mostly 15–60 cm. tall. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: On high sandy and gravelly hills near the junction of the Snake and Clearwater Rivers, vicinity of Lewiston, Idaho (either in Washington or in Idaho), approximately 24 July 1826, *D. Douglas* (K; isotype, BM).

DISTRIBUTION (Figure 69): Sandy flats or steep, loose slopes, in Adams, Whitman, and Walla Walla Counties, southeastern Washington, west along the Columbia River to Klickitat County and Hamilton Island, Skamania County, Washington; Washington, Canyon, Owyhee, and Jerome Counties, southwestern Idaho; south through eastern Oregon (Grant, Harney, and Malheur Counties); and again in west-central Nevada (southern Washoe, western Churchill, easternmost Lyon, and Mineral Counties) and adjacent Mono County, California, in the vicinity of Mono Lake and Benton. Indistinguishable populations occur in the vicinity of Toroweap Valley, Mohave County, Arizona (e.g., *Cottam* 13936, CAS, UT). From 2,000–7,500 ft. alt.

Vouchers for chromosome number (3 individuals, 3 populations), $n=7$:

U.S.: NEVARA: MINERAL CO.: W. side of Walker L., R11246 (7 pairs). WASHOE CO.: Pyramid L., 18.8 mi. N. Sutcliffe, R13197 (7 pairs); ca. 15 mi. N. of Nixon, ca. 3,500 ft., *Ornduff* 4203 (LA; 4 pairs + ring of 6).

Camissonia boothii subsp. *boothii* occurs in three disjunct areas, intergrading completely with subsp. *intermedia* and subsp. *alyssoides* in the Nevada portion of its range. A few collections from two areas on the Mojave Desert of California, within the range of subsp. *desertorum*, resemble subsp. *boothii* closely in their glandular pubescence, habit, and summer blooming:

U.S.: CALIFORNIA: INYO CO.: 10 mi. N. of Little Lake, 1931, *Hoffmann* 576 (POM). SAN BERNARDINO CO.: Brown's Crossing of the Mohave R., 1882, *S. B. & W. F. Parish* 1504 (DS, F, GH); Hesperia, 1901, *Abrams* 2166; near Victorville, 1916, *Peirson* 792 (RSA).

Plants of this sort have not been collected in these areas for nearly 40 years. The relationship of these populations to the other subspecies should be investigated when additional material becomes available. It is possible, but seems unlikely, that the plants were introduced in these areas. A similar specimen has been seen from Fort Mojave, Mohave County, Arizona, 1860–1861, *Cooper* (GH).

Self-incompatibility was demonstrated in 40 plants from the locality of R11246, cited above, by examining pollen-tube growth in selfed and outcrossed stigmas.

55. Camissonia pygmaea (Dougl.) Raven, Brittonia 16: 285. 1964.

FIGURES 71–73

Oenothera pygmaea Dougl., *in* Hook., Fl. Bor. Amer. 1: 213. 1834.

Oenothera boothii var. *pygmaea* (Dougl.) Torr. & Gray, Fl. N. Amer. 1: 510. 1840.

Sphaerostigma boothii var. *pygmaeum* (Dougl.) Walp., Rep. 2: 78. 1843.

Very similar to *C. boothii* subsp. *boothii*, the plants 1.5–35 cm. tall. Flowers smaller, the hypanthium 1.7–2.2 (–4) mm. long, 0.8–1 (–1.5) mm. across at the summit; sepals 1.8–2 mm. long, 0.9–1 mm. wide; petals 1.5–2.5 mm. long, 0.8–1.3 (–2) mm. wide; filaments of episepalous stamens 1–2.2 mm. long, those of the epipetalous ones slightly shorter, the anthers 0.45–0.5 (–0.7) mm. long; style 3.2–4 mm. long, the stigma 0.5–0.8 mm. thick, surrounded by the anthers at anthesis. Gametic chromosome numbers, $n=7$, 14. Autogamous.

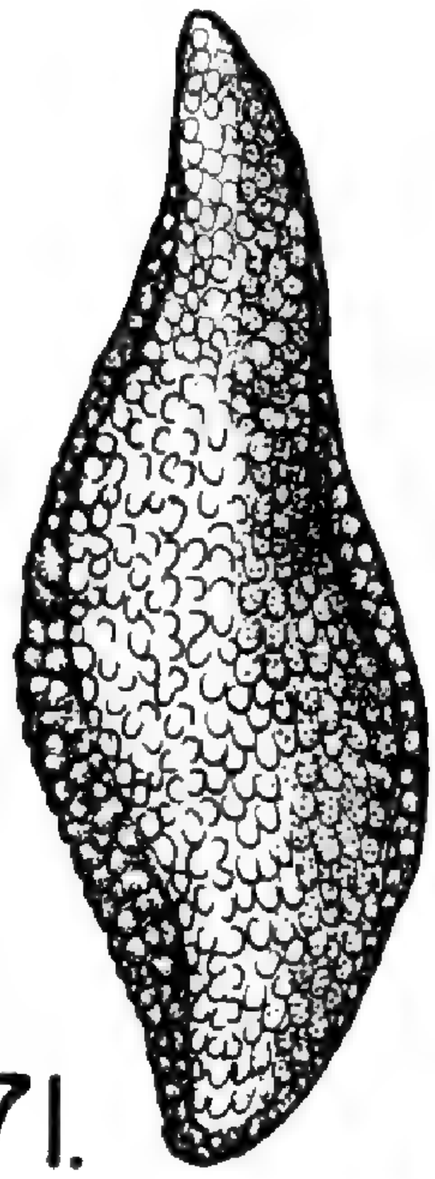
TYPE: On the barren sands of the interior near the Umatilla ("Utalla") River, east of Pendleton, Umatilla County, Oregon, June 1826, *D. Douglas* (K; isotype, BM).

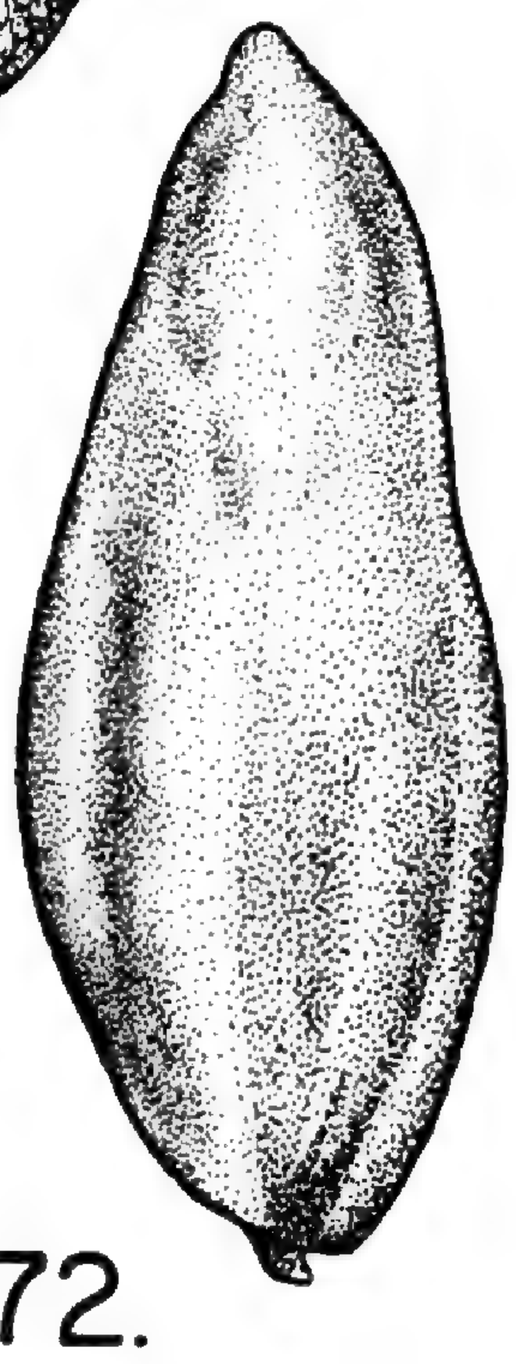
DISTRIBUTION (Figure 68): Rare and local on steep, loose slopes, often in scree, sometimes on gravelly flats, at scattered localities in eastern Washington (Douglas, Grant, and Kittitas Counties), eastern Oregon, and at one locality in adjacent southern Idaho (Jerome County). From 1,200–4,000 ft. alt.

Voucher for chromosome number (1 individual), $n=7$:

U.S.: OREGON: WHEELER CO.: 10 mi. NW. of Mitchell, R18474.

Voucher for chromosome number (1 individual), $n=14$:





FIGURES 70–73.—Species of *Camissonia* sect. *Eremothera:* 70, *C. gouldii*, × ¾ (*Gould* 1423, holotype, POM). 71–73, *C. pygmaea* (*Henderson* 5411, DS): 71–72, Seeds, × 36: 71 dark papillose seed from lower part of capsule; 72, lighter, smoother seed from upper part of capsule. 73, Flowering branch, × ¾.

U.S.: WASHINGTON: GRANT CO.: Dry Falls, R18489 (12 pairs + ring of 4).

ADDITIONAL SPECIMENS EXAMINED:

U.S.: IDAHO: JEROME CO.: Blue Lakes, Snake Plains, 1893, *Palmer* 71 (CAS, UC), 523 (CAS, UC; these two collections with relatively large flowers and doubtfully referred here). OREGON: GILLIAM CO.: Near camp on Pine Creek, 1470 m, *Leiberg* 199 (F, GH, NY, ORE, UC, US). GRANT CO.: Muddy Station, John Day Valley, *T. Howell* in 1885 (F, GH, NY, ORE, PH, US, WS, WTU); John Day Valley NW. of Dayville, *Ripley & Barneby* 6628 (CAS, NY); Squaw Creek, Humphreys Ranch, *Henderson* 5411 (CAS, DS, GH, ORE); 5 mi. W. of Mt.

Vernon, Peck 19880 (CAS). HARNEY CO.: Base of Steens Mt., *T. Howell* in 1885 (NY). WHEELER CO.: Dry gravelly washes between Sutton Mt. and Bridge Creek, 10 mi. NW. of Mitchell, 2,200 ft., *Cronquist* 7239 (CAS, DAO, DS, GH, NY, RM, UBC, UC, WS, WTU); 17 mi. E. of Mitchell, *Peck* 21056 (UC); 22 mi. E. of Mitchell, R18480 (DS). WASHINGTON: DOUGLAS CO.: Rock Island, *Sandberg & Leiberg* 441 (CAS, GH, LE, NMC, ORE, PH, POM, UC, US, WS, WTU). GRANT CO.: Dry Falls, *Thompson* 9105 (DS, GH, NY, POM, RSA, UC, US, WTU); Grand Coulee near Park Lake, *Thompson* 11657 (WTU); Soap Lake, *Eyerdam* 642 (UC). KITTITAS CO.: Above Blue Lake, near Cle Elum, *McCalla* 4438 (UBC).

This rarely collected species is obviously an autogamous derivative of populations similar to those of the much larger flowered, self-incompatible *C. boothii* subsp. *boothii*. As mentioned in the list of cited specimens, the occurrence of *C. pygmaea* in Idaho is somewhat doubtful and needs to be confirmed. I have been unable to separate diploid and tetraploid populations of this species morphologically or by any character of the pollen. It is likely that the tetraploid individual examined was of autopolyploid origin, and the observation of a ring of four chromosomes in it tends to confirm this view. This plant was the only tetraploid invidudual found in the section.

56. Camissonia gouldii Raven, sp. nov. FIGURE 70

A *C. pygmaea* persimilis, differens pilis omnibus glandulosis; foliis ellipticis; capsulis 8–12 mm. longis, 1.7–1.8 mm. latis; seminis omnibus sublaevibus, nullis papillosis. Autogama.

TYPE: Associated with *Phacelia palmeri*, on steep slope of volcanic cone among loose cinders, Diamond Valley, 12 miles north of St. George, 3,500 ft., Washington County, Utah, 15 October 1941, *Frank W. Gould* 1423 (POM; isotypes, ARIZ, CAS, F, GH, NY, UC, US).

DISTRIBUTION (Figure 68): Volcanic scree or cinder flats, rare and local; south-central Washington County, Utah, and east-central Coconino County, Arizona; 3,500–5,400 ft. alt.

ADDITIONAL SPECIMENS EXAMINED:

U.S.: ARIZONA: COCONINO CO.: Cinder flats E. of San Francisco Peaks, 1,700 m., *Leiberg* 5808 (US); San Francisco Mt., *Knowlton* 200 (US). WUPATKI NATL. MONUMENT (COCONINO CO.): Deadmans Wash below Wupatki Ruin, occasional on volcanic ash, ca. 4,800 ft., *Whiting & Jones* 1089/5213 (US); Wupatki Rim, *Jones* 337 (ARIZ); E. slope of Doney Mt., 2 mi. W. of Wupatki, deep cinder soil, 5,200 ft., *Jones* in 1939 (ARIZ); deep cinder near Hall Canyon, 5,400 ft., *Whiting* 1089/5274 (ARIZ, POM).

Camissonia gouldii is obviously autogamous and, like *C. pygmaea*, probably a derivative of populations similar to those of the self-incompatible *C. boothii* subsp. *boothii*. The monomorphic seeds and entirely glandular pubescence of *C. gouldii* (fig. 70) set it off from *C. pygmaea*, the nearest stations of which are some 500 miles to the

northwest. In addition, its reddish color and relatively broad leaves give *C. gouldii* a very distinctive aspect. The chromosome number of *C. gouldii* is unknown.

It is a pleasure to name this distinctive local endemic in honor of Prof. Frank W. Gould of Texas A. & M. University, student of the grasses, who has collected widely and critically in the western United States, in Mexico, and elsewhere in Latin America. It adds another to the long list of edaphically sharply restricted endemics of its region, one of which is *Camissonia parryi*.

57. Camissonia nevadensis (Kell.) Raven, Brittonia 16: 285. 1964. FIGURE 74

Oenothera nevadensis Kell., Proc. Calif. Acad. 2: 224, *fig. 70.* 1863.

Sphaerostigma tortuosa A. Nels., Proc. Biol. Soc. Wash. 17: 95. 1904. Type: Truckee Pass, Virginia Mts., Washoe Co., Nev., 16 June 1902, *P. B. Kennedy* 766 (RM; isotypes, DS, UC).

Oenothera gauraeflora var. *caput-medusae* H. Lév., Monogr. Onoth. 226. 1905. Lectotype: Foothills, Reno, 5,500 ft., Washoe Co., Nev., 10 June 1897, collector unknown (MO; isotypes, POM, UC, US).

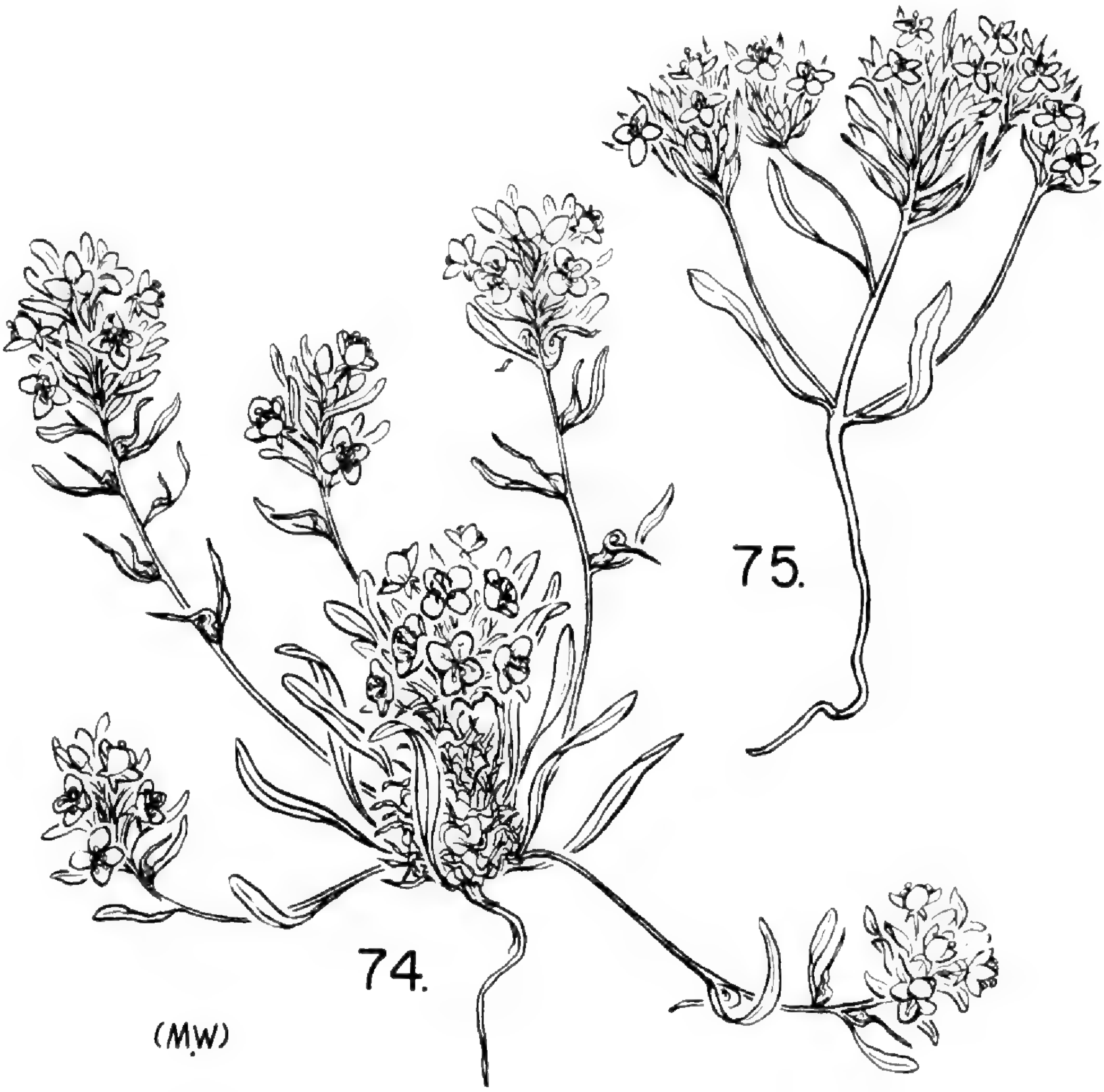
Oenothera gauraeflora var. *vermiculata* M. E. Jones, Contr. West. Bot. 12: 16. 1908.

Sphaerostigma nevadense (Kell.) Heller, Muhlenbergia 6: 51, with cover illustration. 1910.

Erect, densely flowering from the base, the central stem 1–5 cm. tall, the larger individuals with slender decumbent branches to 18 cm. long radiating from near the base of the plant, these naked below and with a dense tuft of leaves and flowers at the ascending end; plants subglabrous, the inflorescence strigulose. Leaves oblanceolate or narrowly oblanceolate, the blades 1–3.5 cm. long, 2–7 mm. wide, entire, acuminate at the apex, attenuate at the base; petioles 1–3 cm. long. Inflorescence erect. Hypanthium 2.2–3.2 mm. long, 1.2–1.3 mm. across at the summit, glabrous within. Sepals 3.2–3.5 cm. long, 1–1.1 mm. wide. Petals 3–5 mm. long, 2.2–4.2 mm. wide. Filaments of the episepalous stamens 4.5–4.8 mm. long, those of the epipetalous ones 3–4 mm. long; anthers 0.4–1.5 mm. long. Style 6–7 mm. long, glabrous; stigma 0.5–0.8 mm. thick, held somewhat above the anthers at anthesis. Capsule highly contorted, 0.8–1.4 cm. long, 1–2 mm. thick near the base, quadrangular in transection, tapering strongly from the swollen base, with a prominent pale brown midrib running down the center of each valve, held on the dead plant and shedding seeds very tardily. Seeds monomorphic, 1.2–1.5 mm. long, 0.3–0.4 mm. thick, gray, finely lacunose, much distorted by the walls of the capsule. Gametic chromosome number, $n=7$. Probably outcrossing, and possibly self-incompatible.

TYPE: From an unknown locality (doubtless the vicinity of Reno, Washoe County, Nevada), CAS 838 in part (fragment).

DISTRIBUTION (Figure 68): Local and colonial on vernally moist clay flats in west-central Nevada, southernmost Washoe, Ormsby,



FIGURES 74–75.—Species of *Camissonia*, × ¾: 74, *C. nevadensis* (*Raven* 17869, DS); 75, *C. hilgardii* (*Raven* 18485, DS).

Storey, northernmost Lyon, and western Churchill Counties; 3,900–4,600 ft. alt.

Voucher for chromosome number (1 individual), $n=7$ (7 pairs):

U.S.: NEVADA: WASHOE CO.: 2 mi. N. of Sparks, R17869 (DS).

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: NEVADA: CHURCHILL CO.: Fallon, *Ross* in 1914 (JEPS); ca. 8 mi. NW. of Fallon, toward Soda L., *Mills & Beach* C–108 (RSA, UC). LYON CO.: 5 mi. S. of Fernley on U.S. Hwy. 95A, *Mason* 15189 (UC). ORMSBY CO.: Empire City, *Jones* 3862 (CAS, GH, NY, POM, RM, UC, US); hills N. of Carson City, *Stretch* in 1865 (NY). STOREY CO.: 13 mi. E. of Sparks, *Goodner & Henning* 4 (POM). WASHOE CO.: University Heights, Reno, 4,550 ft., *Heller* 9697 (DS, GH, PH, UC); 12 mi. N. of Reno on road to Pyramid Lake, 4,000 ft., *Ripley & Barneby* 4492 (CAS, NY); Truckee Pass E. of Reno, 4,500 ft., *Heller* 8647 (DS, GH, NY, PH, US), *Kennedy* 1592 (NY, UC, US); near Wadsworth, *Kennedy* 2053 (DS); 9 mi. N. of Poeville, 5,200 ft., *Tillotson* 120 (RSA, UC); 2.6 mi. NW. of Spanish Spring, 4,500 ft., *Hendrix* 823 (RSA, UC); 6 mi. SW. of Reno, *Canby* 99 (POM); 2 mi. N.

of Sparks on Pyramid L. road, 4,700 ft., *Archer* 5077 (POM); near Pyramid L., Lemmon 239 (F; locality may be only an approximation).

Mature plants of this species are unmistakable; occasionally younger ones are identified as *Camissonia boothii* subsp. *alyssoides*. The habitats of these two taxa are distinct, and *C. nevadensis* is not known to occur sympatrically with any other member of its section. Floral morphology suggests that *C. nevadensis* is outcrossed, but it is not known whether this species is self-incompatible. It probably is not, judging from what is known of the other local entities within the genus and the tribe. *Camissonia nevadensis*, one of the two species of its genus endemic to Nevada (the other *C. megalantha*), is relatively rare, and a number of its localities are being destroyed by urban expansion in the vicinity of Reno. A few collections made by J. G. Lemmon suggest the occurrence of this species in adjacent California, but Lemmon's localities are notoriously inaccurate, and it would seem to be much more probable that he obtained this material in the vicinity of Reno or Pyramid Lake, where he is known to have collected the species.

58. Camissonia minor (A. Nels.) Raven, Brittonia 16: 285. 1964. FIGURE 76

Oenothera alyssoides var. *minutiflora* S. Wats., Bot. King Rep. 111. 1871. Lectotype: Stansbury I., 2,300 ft., Tooele Co., Utah, June 1869, *S. Watson* (US: isotype, NY); non Fisch. & Mey. 1835.

Sphaerostigma minus ("*minor*") A. Nels., Bull. Torrey Cl. 26: 130. 1899.

Sphaerostigma nelsonii Heller, Muhlenbergia 1: 1. 1900, nom. subs.

Oenothera chamaenerioides var. *torta* H. Lév., Monogr. Onoth. 230. 1905. Lectotype: Granger, Sweetwater Co., Wyo., 3 June 1898, *A. Nelson* 4691 (MO; isolectotypes, F, GH, NY, RM, UC, US).

Sphaerostigma tortum (H. Lév.) A. Nels., Bot. Gaz. 40: 60. 1905.

Sphaerostigma tortum var. *eastwoodae* A. Nels., Bot. Gaz. 40: 61. 1905. Type: Grand Junction, Mesa Co., Colo., May 1892, *A. Eastwood* (MO; isotypes, GH, NMC, NY, OSC, UBC, US).

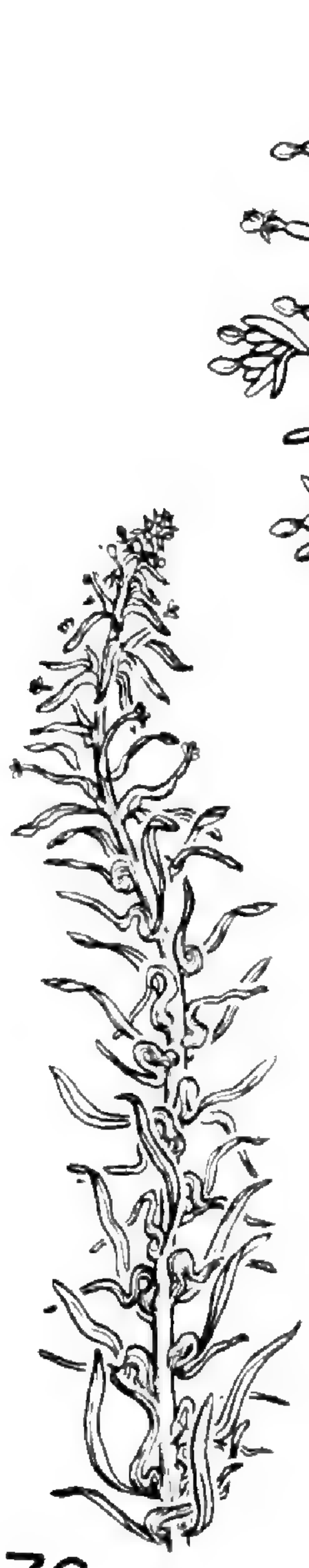
Sphaerostigma alyssoides var. *minutiflorum* (S. Wats.) Small, Bull. Torrey Cl. 33: 146. 1906.

Oenothera minor (A. Nels.) Munz, Bot. Gaz. 85: 238. 1928.

Oenothera minor var. *typica* Munz, Bot. Gaz. 85: 239. 1928.

Oenothera minor var. *cusickii* Munz, Bot. Gaz. 85: 240. 1928. Type: Malheur R. and adjacent hills, Malheur Co., Oreg., 6 June 1901, *W. C. Cusick* 2545 (UC 35348; isotypes, F, GH, K, NY, POM, RM, UC, US).

Erect, flowering from the base, and often well branched from below, the stems 3–30 cm. long; plants densely strigulose, often grayish, the inflorescence often with a more or less evident admixture of glandular trichomes. Leaves oblanceolate or narrowly oblanceolate, the blades of the basal leaves 0.5–2.5 cm. long, 0.3–1.5 cm. wide, the petioles 5–20 mm. long; leaves acuminate at the apex, attenuate at the base. Inflorescence erect. Hypanthium 0.5–1.9 mm. long, 0.5–1.2 mm. across at the summit, pubescent in lower half within. Sepals 0.8–1.8 mm. long, 0.35–0.7 mm. wide. Petals 0.8–1.3 mm. long, 0.4–1.3 mm. wide. Filaments 0.3–1.3 mm. long, the epipetalous ones



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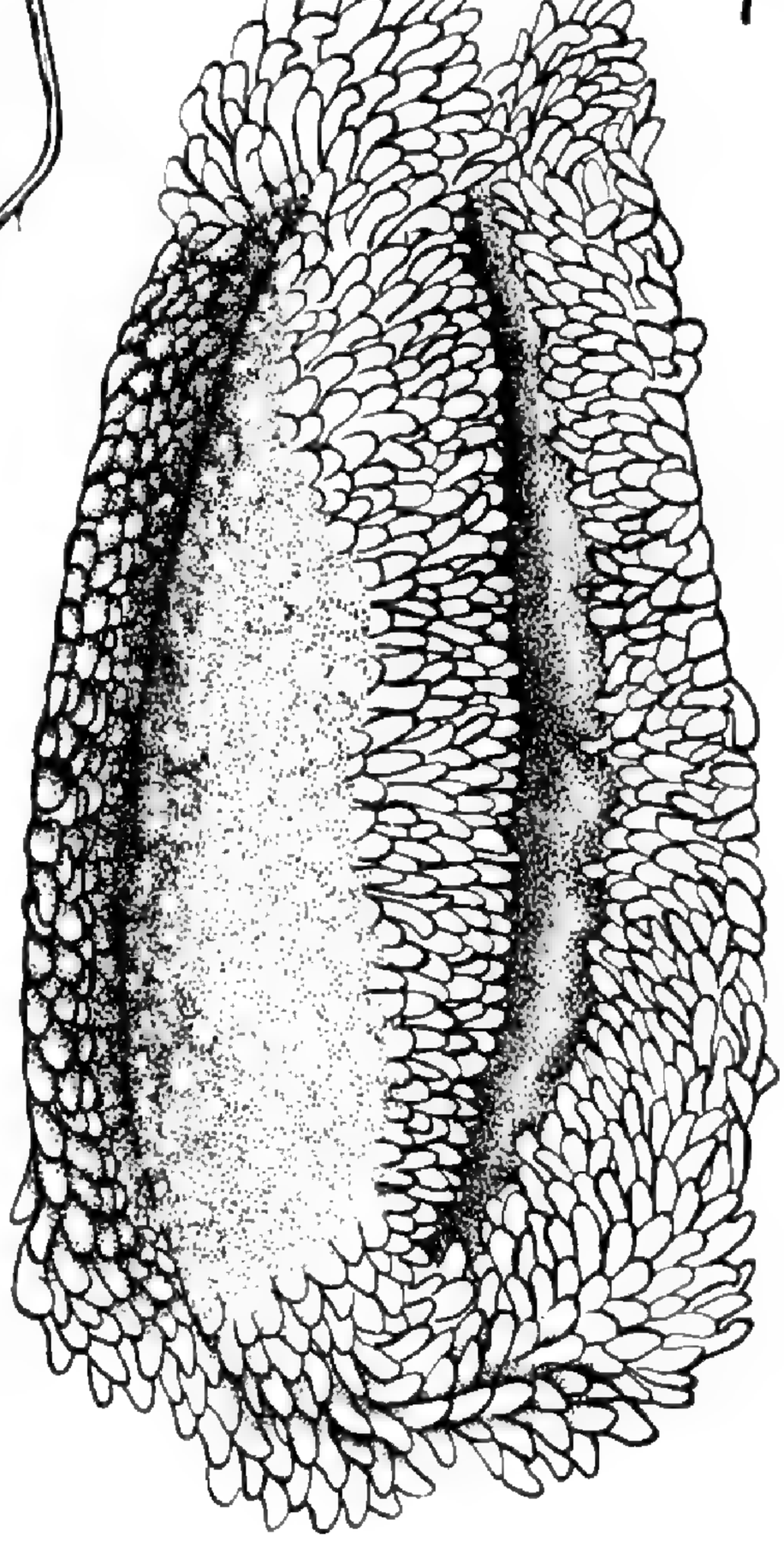

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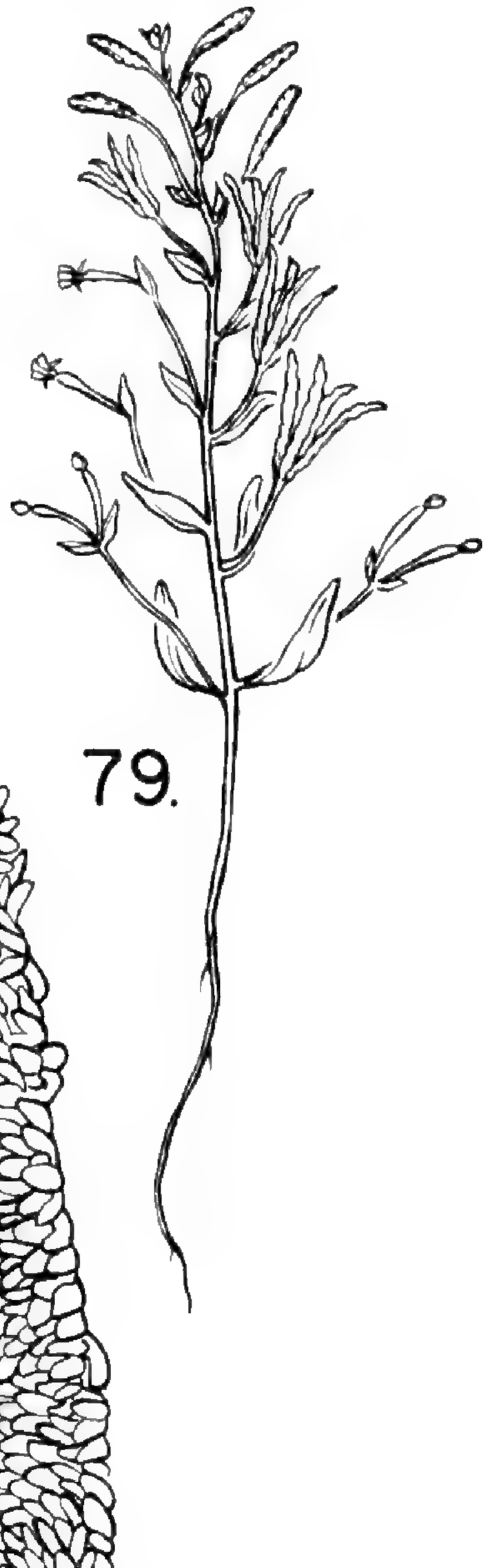

79.

(M.W)

FIGURES 76–79.—Species of *Camissonia:* 76, *C. minor*, × ¾ (*Train* 191, DS). 77–79, *C. pterosperma:* 77, Habit, × ¾ (*Leiberg* 2075, DS); 78, ventral view of winged seed, × 65 (*Heller* 8376, DS); 79, habit of fruiting plant, × ¾ (*Heller* 8376, DS).

shorter than the episepalous ones and sometimes apparently abortive; anthers 0.5–0.8 mm. long. Style 1.2–3.2 mm. long, pubescent near the base; stigma 0.5–0.6 mm. thick, surrounded by the anthers at anthesis. Capsule contorted, 1–2.5 cm. long, 0.8–1.2 mm. thick, subterete, not tapering sharply. Seeds monomorphic, 1.1–1.2 mm. long, 0.4–0.45 mm. thick, gray, finely lacunose. Gametic chromosome number, $n=7$. Autogamous or rarely cleistogamous.

TYPE: Green River, Sweetwater County, Wyoming, 31 May 1897, *A. Nelson* 3047 (RM; isotypes, GH, NY, US).

DISTRIBUTION (Figure 80): Occasional on sandy slopes and flats, often with *Artemisia tridentata*, from Douglas and Lincoln Counties, eastern Washington; Payette, Lehmi, Butte, and Bannock Counties, southern Idaho; and Wyoming (Big Horn, 12 miles north of Graybull, 4,050 ft., *Hamner* 43, RM; Washakie, west of Worland, 4,100–4,300 ft., *Nichols* 374, RM; Sweetwater; and Carbon Counties) south through southeastern Oregon (Lake, Harney, and Malheur Counties), Utah (south to Beaver, Sevier, San Pete, Duchesne, and Uintah Counties), and westernmost Colorado (Moffat and Mesa Counties) to northern and central Nevada (Humboldt, White Pine, Eureka, Elko, Pershing, Lander, Nye, and Washoe—near Verdi, *Stokes* in 1903, US—Counties), and northeastern California (valley east of Cedarville, 4,000 ft., Modoc County, *Ripley & Barneby* 6006, CAS).

Vouchers for chromosome number (3 individuals, 3 populations), $n=7$ (all 7 pairs):

U.S.: NEVADA: EUREKA CO.: Near Lone Mt., cultivated at Los Angeles, R15418. OREGON: HARNEY CO.: 4.7 mi. S. of Narrows, R18443; 12.9 mi. S. of Narrows, R18448.

This species is here taken in the same sense in which it was constituted by Munz (Bot. Gaz. 85: 238–240) in 1928. Some of the populations from the western portions of the range of this species consist of relatively small-flowered individuals, but these do not constitute the sort of well-marked geographical race that I consider to merit formal taxonomic recognition. Thus I do not recognize the taxon described as *Oenothera minor* var. *cusickii*.

In some of the plants of *Hitchcock & Muhlick* 21200 (DS), from 21 miles north of French Glen, Harney County, Oregon, the epipetalous stamens are extremely reduced, the apparently abortive anthers being subsessile. It is conceivable that some plants of this species might be found which lack this set of anthers completely, as is the case in some populations of *C. andina* and in both known populations of *C. exilis*. In these cases, it would appear that the drastic reduction or loss of the smaller set of anthers is associated with autogamy; in the other genus of the tribe Onagreae containing species in which there has been a loss of the epipetalous stamens, namely *Clarkia*, this is certainly not the case.

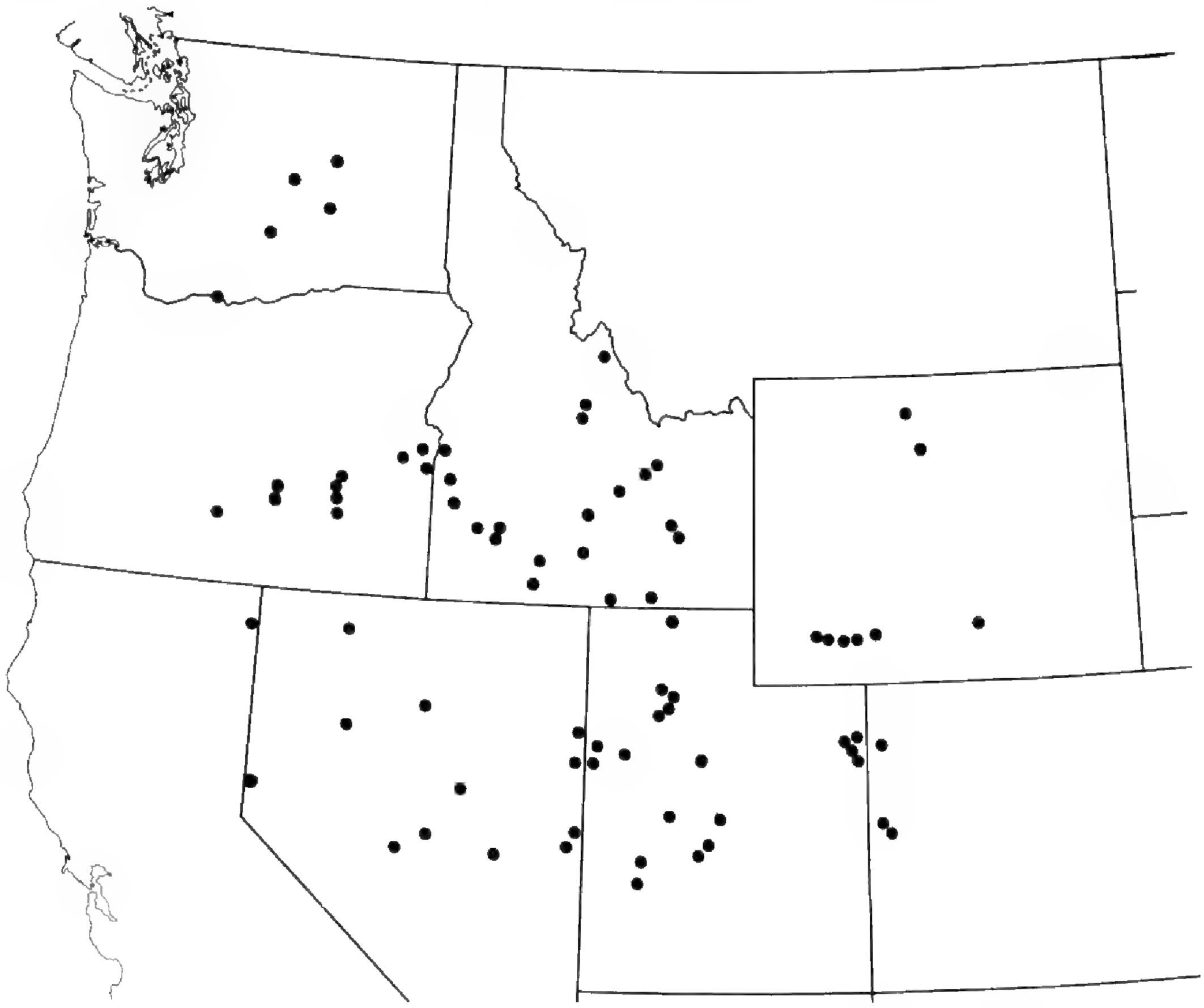

FIGURE 80.—Western United States, showing range of *Camissonia minor*.

Section VIII. *Chylismiella*

Camissonia sect. *Chylismiella* (Munz) Raven, Brittonia 16: 282. 1964.
Oenothera sect. *Chylismiella* Munz, Amer. Journ. Bot. 15: 224. 1928.
Oenothera subg. *Chylismia* sensu Munz, Amer. Journ. Bot. 15: 224. 1928.

Annuals, the plants caulescent, not flowering at the basal nodes, the leaves cauline; plants with exfoliating white rhytidome. Leaves subsessile, sometimes purple-dotted. Inflorescence nodding at anthesis, becoming erect in fruit. Flowers opening near sunrise. Ovary lacking a sterile projection. Petals white, yellow at the base, fading purplish after fertilization, without any dots or other markings. Stamens, style, and inside of hypanthium yellow. Pollen shed singly. Capsule stalked, regularly and promptly loculicidal, straight, or slightly curved, somewhat torulose, terete, the seeds in two rows in each locule, appearing as one by crowding. Seeds monomorphic, brown, with a convex side and a concave side, the concave side surrounded by a thick wing, this and the back densely covered with glassy, clavate trichomes.

TYPE SPECIES: *Camissonia pterosperma* (S. Wats.) Raven.

DISTRIBUTION: Southeastern Oregon, south through Nevada and western Utah to Inyo County, California, and northern Coconino and Mohave Counties, Arizona.

The single species of this section is extremely distinctive and cannot be allied with any other group of the genus with confidence. There is no

reason to consider it related to sect. *Chylismia*, the only common feature being the prominently stalked capsule. The color of the petals, white with a yellow band near the base, is unique in *Camissonia* but widespread in the related genus *Gayophytum* and found nowhere else in the tribe Onagreae.

59. Camissonia pterosperma (S. Wats.) Raven, Brittonia 16: 282. 1964.
FIGURES 77–79

Oenothera pterosperma S. Wats., Bot. King Rep. 112, *pl. 14*. 1871.
Chylismia pterosperma (S. Wats.) Small, Bull. Torrey Cl. 23: 193. 1896.
Sphaerostigma pterospermum (S. Wats.) A. Nels., Bot. Gaz. 40: 63. 1905.

Slender and branching freely, 2–14 cm. tall; stems and leaves entirely covered with hispid pubescence. Leaves narrowly lanceolate to oblanceolate, 0.3–3 cm. long, 0.1–0.6 cm. wide, entire, with a single prominent vein, acute or acuminate at the apex, the base narrowly cuneate or attenuate. Inflorescence glandular pubescent. Hypanthium 1–2 mm. long, 1–1.2 mm. across at the summit, glabrous within. Sepals 1.5–2.5 mm. long, 0.8–1.2 mm. wide. Petals 1.5–2.5 mm. long, 1–1.9 mm. wide. Filaments of the episepalous stamens 1–1.7 mm. long, those of the epipetalous ones 0.5–1 mm. long; anthers 0.3–0.4 mm. long. Style 2.2–4 mm. long, glabrous; stigma 1–1.5 mm. thick, surrounded by the anthers at anthesis. Capsule 1.2–1.8 cm. long, 1.2–1.6 mm. thick, ascending or spreading; pedicel 4–8 mm. long, spreading. Seeds 1–1.5 mm. long, 0.6–0.8 mm. thick, broader at one end, and truncate at each end (where contacting next seed in row), the trichomes longer at one end than at the other and shortest in the middle, the two areas of trichomes (back and wings) separated by a narrow glabrous band running around the seed. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Growing under sagebrush, Trinity Mountains, 5,000 ft. (probably Churchill County), Nevada, May 1868, *S. Watson* (US 47918; isotypes, GH, NY).

DISTRIBUTION: Well-drained slopes, often of volcanic orgin, with *Pinus edulis*, *Juniperus*, and *Artemisia tridentata*, from south-eastern Oregon (Lake and Malheur Counties) south through Nevada and western Utah to Inyo County, California, and northern Mohave and Coconino (upper end of House Rock Valley, *Goodding* 112–49, RM) Counties, Arizona; widely distributed but rare. From 2,500–8,000 ft. alt. See Univ. Calif. Publ. Bot. 34:*fig. 2*. 1962.

Section IX. *Nematocaulis*

Camissonia sect. *Nematocaulis* Raven, Brittonia 16: 285. 1964.
Oenothera subg. *Sphaerostigma* sensu Munz, Bot. Gaz. 85: 234. 1928; pro parte.
Oenothera sect. *Nematocaulis* (Raven) Munz, N. Amer. Fl. II. 5: 155. 1965.

Annuals, the plants caulescent, flowering from near the base, but the lower stem usually naked, the leaves cauline and densely tufted,

nearly every one bearing a flower in its axil; many slender branches often arising from near the base, these naked below, the leaves and flowers tufted near the end of each as on the main stem. Leaves subsessile. Inflorescence erect. Flowers opening near sunrise. Ovary lacking a sterile projection. Petals yellow, not fading purplish after fertilization, without any dots or other markings. Stamens, style, and inside of hypanthium yellow. Stamens eight, the epipetalous ones sometimes greatly reduced, or four. Pollen shed singly. Capsule sessile, regularly loculicidal, straight or nearly so, somewhat torulose, strongly flattened, the central axis falling free at maturity, the seeds in one row in each locule, crowded. Seeds monomorphic, narrowly obovoid, light to dark brown, smooth and shining.

TYPE SPECIES: *Camissonia hilgardii* (Greene) Raven.

DISTRIBUTION: Southern British Columbia and Alberta, south through westernmost Montana, western Wyoming, eastern Washington, and eastern Oregon to northern and central Utah and Nevada and northeastern California, east of the Cascade axis.

The two species assigned to this section are very closely related but entirely distinct within the genus; they are not similar to any other group with which I am familiar. The smaller flowered tetraploid and hexaploid populations, comprising *Camissonia andina*, have an extremely wide distribution, whereas the larger flowered diploids, *C. hilgardii*, have a relatively narrow range almost entirely in eastern Washington. On the basis of present knowledge of the group, it would appear likely that the tetraploids have had an autopolyploid origin, and that the hexaploids may have been derived directly from them by the functioning of an unreduced gamete. Such a hypothesis would if true postulate the existence of strict genetic control of pairing in this group, as no multivalents have been observed at diakinesis and metaphase I in the polyploids; but this must be true of the members of sect. *Holostigma* and sect. *Camissonia*, so it may also apply here. As there is only one series of diploid populations known in this extremely distinct group, no alternative seems to suggest itself.

Occasional plants of the highly autogamous, sometimes even cleistogamous, member of sect. *Nematocaulis*, *Camissonia andina*, have 3-merous flowers; these have been named *Oenothera andina* f. *tripetala* by Léveillé and *O. andina* var. *anomala* by M. E. Peck. Such flowers are unknown elsewhere in the genus but appear again in another genus of the tribe, *Gaura*, where they characterize one autogamous entity, *G. hexandra* Gómez Ortega subsp. *hexandra*, and are found very frequently in another autogamous species, *G. angustifolia* Michx. Elsewhere in the family 3-merous flowers occur regularly only in the highly autogamous (sometimes cleistogamous) African *Ludwigia* sect. *Prieurea*, consisting of a single variable species. Thus

there appears to be a strong correlation between autogamy and the reduction in number of flower parts in the family Onagraceae. The same may be said of the loss of epipetalous stamens, which occurs in occasional plants (perhaps entire populations?) of *Camissonia andina* (e.g., two from Blaine County, Idaho: *Macbride & Payson* 3056, POM; *Macbride* 806, DS). As noted above, there is a strong tendency toward this condition in some individuals of the highly autogamous *Camissonia minor*, and it is a consistent feature in the two known populations of *C. exilis*. On the other hand, there is certainly no connection between autogamy and the loss of the epipetalous stamens in *Clarkia* or in *Ludwigia*, with a single exception in the latter: relatively small-flowered (and presumably more highly autogamous) individuals and populations of *L. inclinata* (L. f.) Raven tend to have only four stamens and have been named *L. verticillata* and placed in another section of the genus by Munz.

60. Camissonia hilgardii (Greene) Raven, Brittonia 16: 285. 1964. FIGURE 75

Oenothera hilgardi Greene, Bull. Torrey Cl. 10: 41. 1883.
Sphaerostigma hilgardi (Greene) Small, Bull. Torrey Cl. 23: 188. 1896.
Sphaerostigma andinum var. *hilgardii* (Greene) A. Nels., Bot. Gaz. 40: 56. 1905.
Oenothera andina var. *hilgardii* (Greene) Munz, Bot. Gaz. 85: 251. 1928.

Similar to *C. andina*, but the flowers larger. Hypanthium 1.5–2 mm. long, ca. 1.2 mm. across at the summit, sparingly pubescent in lower portions within. Sepals 2–3 mm. long, 0.9–1.1 mm. wide. Petals 2.5–5 mm. long, 2.2–3.5 mm. wide. Filaments of the episepalous stamens 2–4 mm. long, those of the epipetalous ones 1.5–2.8 mm. long; anthers of the longer stamens 0.7–0.8 mm. long, those of the shorter 0.5–0.6 mm. long. Style 4.5–6 mm. long, sparsely pubescent near the base; stigma 0.7–0.8 mm. thick, held at or slightly above the anthers of the longer stamens at anthesis. Gametic chromosome number, $n=7$. Probably self-compatible but outcrossing.

TYPE: Moist alkaline soil of the Klickitat Swale, Klickitat or Yakima County, Washington, July 1882, *E. Hilgard* (GH).

DISTRIBUTION (Figure 81): Sandy or clay slopes under *Artemisia tridentata*, scattered but locally common, occasionally growing with *C. andina*, in Okanagan, Chelan, Douglas, Grant, Kittitas, and Yakima Counties, Washington; collected twice along the lower Columbia River, at Bingen, Klickitat County, Washington, and Hayden Island, Multnomah County, Oregon. From near sea level to ca. 1,600 ft. alt.

Vouchers for chromosome number (2 individuals, 2 populations), $n=7$ (7 pairs in each):

U.S.: WASHINGTON: KITTITAS CO.: 16.7 mi. W. of Ginkgo Petrified Forest, R18485. YAKIMA CO.: 2.3 mi. S. of L. Wenas, R18483.

61. Camissonia andina (Nutt.) Raven, Brittonia 16: 285. 1964.

Oenothera andina Nutt., *in* Torr. & Gray, Fl. N. Amer. 1: 512. 1840.

Sphaerostigma andinum (Nutt.) Walp., Rep. 2: 79. 1843.

Oenothera andina f. *tripetala* H. Lév., Monogr. Onoth. 182. 1905. No specimens cited.

Oenothera andina var. *typica* Munz, Bot. Gaz. 85: 250. 1928.

Oenothera andina var. *anomala* M. E. Peck, Torreya 32: 151. 1932. Type: Dry slope 6 mi. NW. of Paisley, Lake Co., Oregon, 15 July 1927, *M. E. Peck* 15176 (WILLU).

Plants finely strigulose throughout, more densely so in the inflorescence, especially on the ovaries. Branches 1–15 cm. long. Leaves very narrowly oblanceolate, 1–3 cm. long, 0.1–0.25 cm. wide, entire, acuminate at the apex, attenuate at the base. Hypanthium 0.8–2 mm. long, 0.75–1.1 mm. across at the summit, glabrous or more rarely sparsely pubescent in lower half within. Sepals 0.8–2 mm. long, 0.5–1.1 mm. wide. Petals 0.8–2.3 mm. long, 0.6–1.2 mm. wide. Filaments of the episepalous stamens 0.45–2.2 mm. long, those of the epipetalous ones 0.1–0.45 mm. long, the epipetalous stamens rarely lacking; anthers of the longer stamens 0.2–0.45 mm. long, those of the shorter ones 0.08–0.2 mm. long. Style 1.7–3 mm. long, glabrous or more rarely sparsely pubescent near the base; stigma 0.4–0.6 mm. thick, surrounded by the anthers at anthesis. Capsule (0.5–)0.8–1 cm. long, 1–1.3 mm. thick along the wider axis, ascending. Seeds 0.7–1.3 mm. long, 0.3–0.35 mm. thick. Gametic chromosome numbers, $n=14$, 21. Autogamous, more rarely cleistogamous.

TYPE: Dry plains near the Blackfoot River, Bingham or Caribou County, Idaho, 10–12 July 1834, *T. Nuttall* (BM; isotypes, GH, K, NY, PH).

DISTRIBUTION (Figure 81): Vernally moist flats, often in clay soil under *Artemisia tridentata* or in pinyon-juniper association, inconspicuous and often overlooked, from the vicinity of Lake Osoyoos, British Columbia, and Medicine Hat, Alberta, south to Missoula County, Montana (Missoula, *Hitchcock* 2326, CAS, POM, RSA, WS); the western half of Wyoming; Cache, Wasatch, and Beaver Counties, Utah; Elko, Eureka, Humboldt, northern Nye, and Ormsby Counties, Nevada; and from Sierra County, California, north along the east side of the Cascades throughout eastern Oregon and Washington, and west along the Columbia River to Skamania County, Washington; from ca. 1,600–ca. 6,500 ft. alt. I have seen a specimen labeled "Golden City, etc., Colorado," *Greene* in 1873 (US), but the occurrence of *Camissonia andina* in that state needs confirmation.

Vouchers for chromosome number (4 individuals, 4 populations), $n=14$:

U.S.: CALIFORNIA: LASSEN CO.: Near Eagle L., *Ornduff* 4205 (LA). IDAHO: FREMONT CO.: Near St. Anthony, R19560. OREGON: LAKE CO.: W. of Lakeview,

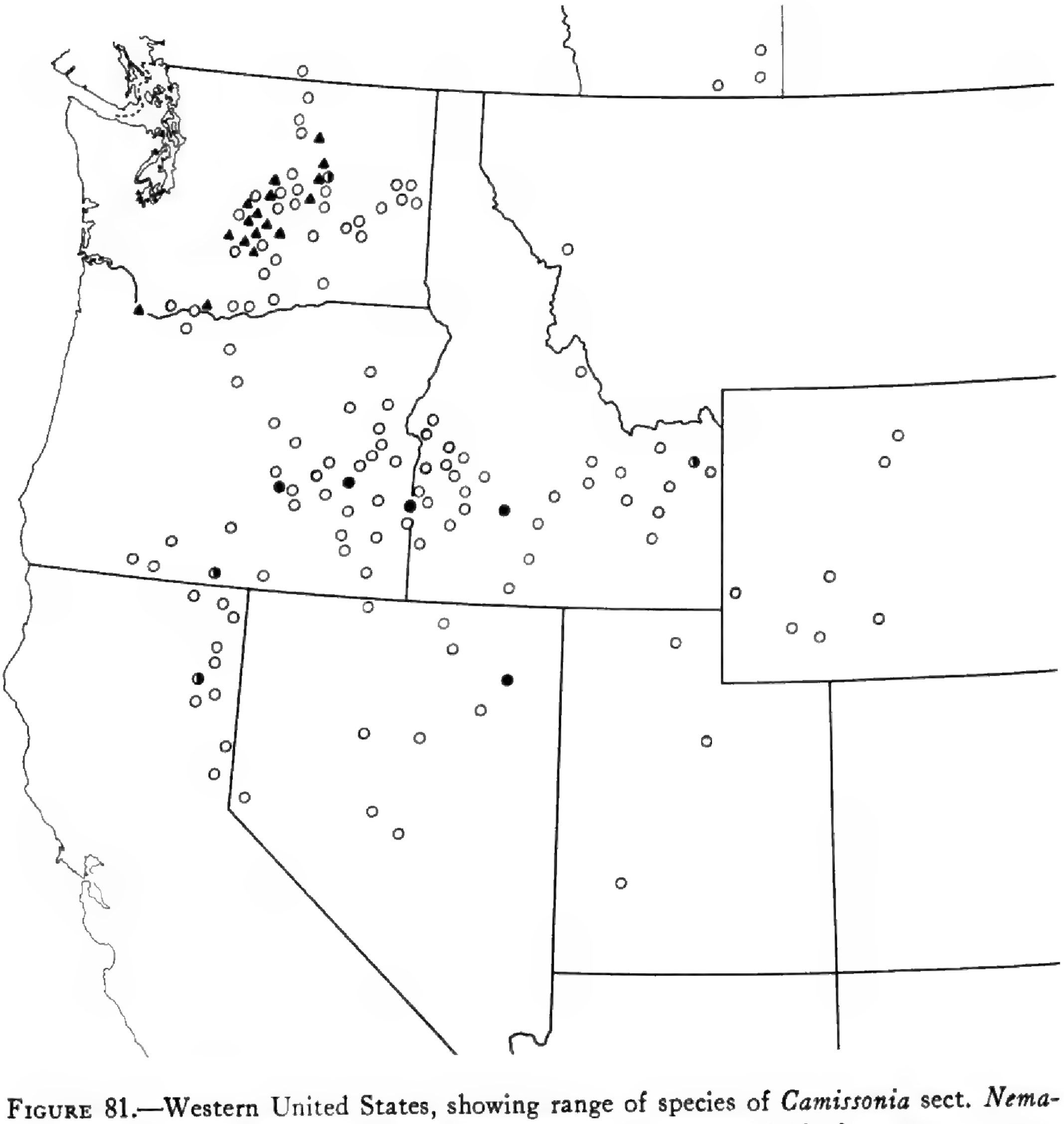

FIGURE 81.—Western United States, showing range of species of *Camissonia* sect. *Nematocaulis:* ▲=*C. hilgardii*; ○=*C. andina*, with ◑=tetraploid chromosome counts (n=14) and ●=hexaploid chromosome counts (n=21).

R18429. WASHINGTON: DOUGLAS CO.: State Hwy. 10, 4.6 mi. N. of junction with U.S. Hwy. 2, R18495.

Vouchers for chromosome number (5 individuals, 5 populations), n=21:

U.S.: IDAHO: ELMORE CO.: 19 mi. E. of Dixie, R18524 (54 percent of pollen 4-pored). NEVADA: ELKO CO.: East Humboldt Mts., R13456. OREGON: HARNEY CO.: 3.4 mi. E. of Buchanan, R18458 (46 percent of pollen 4-pored); 14 mi. NE. of Wagontire, R13356. MALHEUR CO.: Idaho State line on U.S. Hwy. 95, R19581.

Camissonia andina grows sympatrically with its diploid relative, *C. hilgardii*, at a number of localities within the range of the latter. With the accumulation of additional chromosome number determinations from *C. andina*, it should become possible to develop a method for distinguishing tetraploids and hexaploids. Whether it will then

become desirable to accord formal taxonomic recognition to tetratploid and hexaploid populations remains to be seen. In general, it now appears that hexaploids often have 40–90 percent 4-pored pollen grains, tetraploids mostly 10 percent or fewer (often none). Several of the collections examined (without chromosome number determinations) had 10–40 percent 4-pored pollen, and more chromosome counts will be necessary to draw a clear line between plants at the two different polyploid levels. At any rate, it is virtually certain that the type collections of this species is hexaploid ($n=21$), as an isotype (NY) had 27 of the 50 pollen grains examined 4-pored.

The limited amount of evidence now available suggests that tetraploid races occupy the margins of the range of this species and are infrequent in the main portion of its range, where hexaploids appear to predominate. I have thus far been unable to discover any morphological distinctions between the two races other than the pollen difference just discussed.

Excluded Species

Sphaerostigma andinum var. *minutum* A. Nels., Bot. Gaz. 40: 56. 1905=*Gayophytum* sp. (Type: without data, MO).

Oenothera micrantha Presl, Rel. Haenk. 2: 31. 1827; non Hornem. ex Spreng. 1825. Type: Chile, *Haenke* (PR). *Holostigma paradoxum* Spach, Nouv. Ann. Mus. Paris III. 4: 334. 1835. *Sphaerostigma paradoxum* (Spach) Gay, Fl. Chil. 2: 329. 1846. *Chamissonia paradoxa* (Spach) Reiche, Anal. Univ. Chile 98: 482. 1897=*Gayophytum micranthum* Hook. & Arn. (cf. Lewis & Szweykowski, Brittonia 16: 389. 1964).

Appendix

Chromosome numbers of *Camissonia* sect. *Holostigma* [4]

In the following lists are grouped the vouchers for chromosome counts in *Camissonia* sect. *Holostigma*. Collections made by Raven are preceded by *R*, those by Breedlove by *B*, and those by Wedberg by *W*. As usual throughout this paper, vouchers are presumed to be deposited at DS unless some other indication of place of deposit is made. In this section, "SDSC" is used for the herbarium of San Diego State College, where some of the vouchers are deposited; abbreviations for other herbaria are standard. In general, Wedberg counted his own collections and Raven counted the others, often with the assistance of Breedlove.

In addition to the original counts reported here, we have also included 34 counts reported for plants of this group by Lewis, Raven, Venkatesh, & Wedberg (Aliso 4: 73–86. 1958). The only earlier chromosome number determinations for the group appear to be those by Johansen (Amer. Journ. Bot. 16: 595–597. 1929; Proc. Nat. Acad. Sci. U.S. 15: 882–885. 1929) of $n=7$ in "*Sphaerostigma veitchianum*" and "*S. spirale*" (=*Camissonia bistorta* and *C. cheiranthifolia*, respectively), but without any indication of the source of the materials examined.

Including the 34 earlier counts for which voucher specimens are available, a total of 389 individuals from 335 populations have been examined cytologically. These populations represent all 17 taxa recognized for the section, including 14 species and 3 additional subspecies. Cytogenetically, the most striking characteristic of these counts is the almost complete lack of rings of chromosomes such as are associated with the presence of reciprocal translocations. Lewis et al. (1958, p. 80) reported 12 pairs and a ring of 4 chromosomes in one plant of *Camissonia confusa* (*Lewis & Lewis* 1669, LA; as *Oenothera micrantha* var. *ignota*). This ring of 4 chromosomes may have resulted from the presence of a reciprocal translocation, or it may have been because of homology between the pairs of chromosomes involved in it. At any rate, it was the only individual, out of 389 examined, in which such a ring of chromosomes was found. In contrast, reciprocal translocations occurred in over 20 percent of the 676 individuals of *Camissonia* sect.

[4] This work was done in cooperation with Dennis E. Breedlove and Hale L. Wedberg (San Diego State College).

Chylismia that were examined cytologically (Raven, Univ. Calif. Publ. Bot. 34: 20–43, 1962), and similar percentages probably occur in sect. *Eremothera* and are characteristic of other groups of the tribe Onagreae, such as the genus *Clarkia*. In view of the complete absence of reciprocal translocations in natural populations of sect. *Holostigma*, it is also of considerable interest that not one of the 389 individuals of this section (with the possible exception noted above) examined cytologically had a supernumerary chromosome, as compared with the 26 of the 676 individuals of sect. *Chylismia*. This would appear to lend considerable weight to Lewis' (Evolution 5: 142–157, 1951) suggestion of a causal relationship between reciprocal translocation (presumably by occasional misdivision of rings of chromosomes) and supernumerary chromosomes in Onagreae.

It is also noteworthy that little evidence of autopolyploid pairing has been found in the two tetraploids and three hexaploids of this section, even though the diploid species contributing to their formation are obviously extremely closely related. This subject is discussed further on p. 176.

Camissonia bistorta (Nutt. ex Torr. & Gray) Raven, (29 individuals, 22 populations), $n=7$:

U.S.: CALIFORNIA: LOS ANGELES CO.: Point Dume, W13, in 1958, 169 (SDSC), in 1957 (LA), *H* (LA), *Lewis* 1634 (LA); Playa del Rey, WI (LA), 562 (SDSC); Mulholland Drive, Santa Monica Mts., W260 (SDSC). ORANGE CO.: Corona del Mar, W172; 6.5 mi. E. of San Juan Capistrano, R17491 (progeny=R18782); 5.6 mi. NE. of San Juan Capistrano, W178; Dana Point, W176; lower edge of Cleveland National Forest just above San Juan Guard Station, 850 ft., R18783. RIVERSIDE CO.: 6.5 mi. SE. of Hemet, B1896; 5 mi. N. of Alberhill, W3; Upper San Juan Campground, W188 (SDSC); Lake Mathew Road, W196; 5.1 mi. W. of Dripping Springs, R14023; 0.5 mi. NW. of Alberhill, WB (LA); Temescal Canyon, *Lewis* 1630 (2 plants; LA); ca. 2 mi. N. of Aguanga, *Klein* 1300 (RSA). SAN BERNARDINO CO.: U.S. Hwy. 70–99, 0.15 mi. W. of Etiwanda Ave., W26 (LA). SAN DIEGO CO.; La Mesa, W922 (SDSC); 2.2 mi. W. of Campo, R16926; Torrey Pines Park, W211 (SDSC); Balboa Park, San Diego, W213 (SDSC).

BAJA CALIFORNIA. 3 mi. S. of Ensenada, *Klein & Gregory* 1272.

Camissonia cheiranthifolia (Hornem. ex Spreng.) Raimann subsp. **cheiranthifolia** (8 individuals, 8 populations), $n=7$:

U.S.: CALIFORNIA: HUMBOLDT CO.: 8.8 mi. N. of Big Lagoon, *T. & L. Mosquin* 4489. LOS ANGELES CO.: San Clemente I., R17627 (progeny). SACRAMENTO CO.: Brannan I. State Park, near Rio Vista, R20178. SANTA BARBARA CO.: Jalama Beach, R14040; San Miguel I., *Blakley* 5099 (the form called *Oenothera nitida* Greene, at its type locality); Santa Cruz I., Fraser Point, R15312; Santa Rosa I., R14995. SONOMA CO.: Bodega Bay to Bodega Head, R18247.

Camissonia cheiranthifolia subsp. **suffruticosa** (S. Wats.) Raven (7 individuals, 7 populations), $n=7$:

U.S.: CALIFORNIA: LOS ANGELES CO.: Point Dume, R13855 (LA, RSA). SAN DIEGO CO.: S. of Carlsbad, R14027; Torrey Pines State Park, W210 (SDSC). SANTA BARBARA CO.: Devereaux Point, B1766 (UCSB); Goleta Point, R14044. VENTURA CO.: Ventura, R13999.

BAJA CALIFORNIA: 3 mi. S. of Ensenada, R17009 (2 plants).

Camissonia confusa Raven (29 individuals, 22 populations), $n=14$:

U.S.: ARIZONA: MARICOPA CO.: 12.6 mi. E. of Tortilla Flat on State Hwy. 88, 2,700 ft., R17373, 12.9 mi. E., R17375. CALIFORNIA: LOS ANGELES CO.: Native to Rancho Santa Ana Botanic Garden, Claremont, R15535, 17748, 18139. ORANGE CO.: Lower San Juan Campground, Santa Ana Mts., *Lewis* 1642 (LA), W183. RIVERSIDE CO.: Upper San Juan Campground, Santa Ana Mts., W187 (SDSC); Ortega Hwy. 3.9 mi. above its E. base, Santa Ana Mts., 2,400 ft., R17488; Reche Canyon, Loma Linda, 1,900 ft., R17471, 18766; 7.7 mi. E. of Hemet, WO (LA), 198; 10.3 mi. S. of Hemet, W204 (SDSC); 6.6 mi. from Banning on Idyllwild road, *Lewis* 1667 (LA); 7.4 mi. from Banning on Idyllwild road, W303 (SDSC); Hwy. 74 ca. 11 mi. W. of Elsinore, Santa Ana Mts., W191 (SDSC). SAN BERNARDINO CO.: Oak Glen Road 2.5 mi. E. of junction with road from Yucaipa to Mill Creek, San Bernardino Mts., 3,300 ft., R17469; 2.3 mi. W. of Mill Creek Ranger Station, 2,300 ft., R17466 (type collection). SAN DIEGO CO.: 2.7 mi. SE. of Aguanga, 2,400 ft., R17388; 0.6 mi. W. of Banner Queen Store, 3,000 ft., R17422; State Hwy. 79, 2.2 mi. S. of junction with State Hwy. 76, N. of Santa Ysabel, 3,300 ft., R17395; road to Mt. Palomar 3.9 mi. NW. of turn to L. Henshaw, 4,000 ft., R17397; L. Henshaw, 2,800 ft., R17396; 2.5 mi. W. of Julian, *H. & M. Lewis* 1669 (2 plants; LA). SAN LUIS OBISPO CO.: La Panza Campground, 2,000 ft., R16968, 18323. VENTURA CO.: Cow Spring Campground, 17.6 mi. N. of Fillmore, Topatopa Mts., 3,500 ft., B2643.

Camissonia guadalupensis (S. Wats.) Raven subsp. **clementina** (Raven) Raven (3 individuals, 3 populations), $n=7$:

U.S.: CALIFORNIA: SAN CLEMENTE I., LOS ANGELES CO.: Eel Point, R17125 (type collection); beach due W. of Wall 2, R17260; W. side of island opposite Wilson Cove, R17628 (progeny=R18176).

Camissonia guadalupensis subsp. **guadalupensis** (2 individuals, 1 population), $n=7$:

BAJA CALIFORNIA: Arroyo Melpomone, Guadalupe I., *Moran & Ernst* 6737 (2 plants in progeny=R17530, 18175).

Camissonia hardhamiae Raven (3 individuals, 3 populations), $n=21$:

U.S.: CALIFORNIA: SAN LUIS OBISPO CO.: 3 mi. E. of Santa Margarita, R18313; Calf Canyon, 3.7 mi. NE. of Santa Margarita, R18315 (type collection); 4.2 mi. NE. of Santa Margarita, at junction to Parkhill District, R18318.

Camissonia hirtella (Greene) Raven (84 individuals, 76 populations), $n=7$:

U.S.: CALIFORNIA: AMADOR CO.: 1.5 mi. N. of Buena Vista, R18351. FRESNO CO.: Copper Creek Trail, Kings Canyon, 5,500 ft., *Howell* 34332 (progeny=R19082, 19748); Simpson Meadow, Middle Fork of Kings R., *Howell* 33793 (progeny=R18989, 19755); 8 mi. N. of Pine Ridge, B15277. KERN CO.: Black Mt. burn, Greenhorn Mts., *Howell* 18779 (progeny=R18779, 19746); Breckinridge Mt., 7,400 ft., *Twisselmann*, 4704 (progeny=R19080); 3.5 mi. E. of Alta Sierra, Greenhorn Mts., R20249; ca. 1 mi. S. of Havilah, *Lewis* 1344. LAKE CO.: 4 mi. E. of Clear Lake, B5150; 4 mi. NW. of Lower Lake, B4542; 2 mi. NE. of Lower Lake, B4539; Lower Lake, R18241. LOS ANGELES CO.: Santa Monica Mts.: Latigo Canyon Road 0.4 mi. from Mulholland Hwy., W287 (SDSC); Corral Canyon, R17512A; Topanga Canyon, W308; Piuma Road 5.1 mi. NW. of Rambla Pacifica, 700 ft., R15369; Mulholland Hwy. just E. of junction with Decker Road, 1,600 ft., R17516; Saddle Peak Road 0.9 mi. above Stuntz Canyon Road, 2,200 ft., R17510; 0.6 mi. above junction of La Tuna Canyon on road to Saddle Peak, 2,050 ft., R17506; Soledad Canyon, *Lewis* 1677 (LA). MARIPOSA CO.: 3.7 mi. NW. of Coulterville, 2,000 ft., R18347. MONTEREY CO.: Hanging Valley, NW. side of Junipero Serra Peak, B5599. RIVERSIDE CO.: 2 mi. S. of Banning, WM (LA); west of Mountain Center, San

Jacinto Mts., W304, 305 (SDSC); Upper San Juan Campground, Santa Ana Mts., *Lewis* 1655 (LA); Upper San Juan Campground to Hwy. 74, W190 (SDSC); 10.3 mi. S. of Hemet on Hwy. 79, W202 (SDSC); Dripping Springs Campground, 1,700 ft., R17384; Ortega Hwy. 1 mi. above E. base, 1,600 ft., R17487, 3.9 mi. above, R17489; Main Divide Truck Trail at Ortega Hwy., 2,300 ft., R17762 (progeny = R18845); Main Divide Truck Trail 8.1 mi. S. of Santiago Peak, Santa Ana Mts., 4,050 ft., R17760; Vandeventer Flat, San Jacinto Mts., WN–1(LA). SAN BERNARDINO CO.: 1.5 mi. W. of Mill Creek Ranger Station, 2,300 ft., R17467; State Hwy. 30, 2 mi. N. of National Forest Boundary, 2,000 ft., R17465, 4.5 mi. N. of boundary, 2,800 ft., R17464; road to Barton Flats 6.5 mi. N. of Mill Creek, R17926 (cleistogamous). SAN DIEGO CO.: 1 mi. from Santa Ysabel road to Julian, 3,000 ft., W928 (SDSC); Lake Wohlford, R20169; 0.9 mi. from U.S. Hwy. 395 on Deer Springs Road to San Marcos, 700 ft., R17473; State Hwy. 94, 1.5 mi. W. of turn to Tecate, 1,600 ft., R17449; 0.5 mi. E. of Santa Ysabel, 3,300 ft., R17339, 17392, 17393; 1.1 mi. E. of Campo, 2,900 ft., R17444; 1.1 mi. E. of Campo, 2,900 ft., R17442, 17443; 3.7 mi. N. of Cameron Corners on road to Pine Valley, 3,500 ft., R17441; 3.1 mi. from U.S. Hwy. 80 on road to Morena Lake, 3,400 ft., R17440; 1.0 mi. E. of Oak Grove, 2,700 ft., R17389; County Road S6 just S. of turn to Felicita County Park, R16948; 5.6 mi. W. of Campo, 2,600 ft., R17448; 3.8 mi. from turn to Escondido on road to Mt. Palomar, 4,100 ft., R17398; 2.3 mi. S. of Rincon Springs on road to Escondido, cultivated at Stanford, R19076; 3.5 mi. NE. of Lake Wohlford, 1,700 ft., R17404; 8.6 mi. E. of Ramona, 2,800 ft., R17413; 2.5 mi. W. of Santa Ysabel, 3,100 ft., R17416; 2.1 mi. E. of Santa Ysabel 3,700 ft., R17418; 0.6 mi. above Banner Queen Store, R16922, 1.3 mi. W., 3,000 ft., R17419, 0.8 mi. E., R16924; Jamul-Lyons Valley road 0.7 mi. NE. of turn to Camp Barrett, 2,200 ft., R17432; U.S. Hwy. 80, 0.7 mi. W. of Guatay Summit, 4,000 ft., R17436. SAN LUIS OBISPO CO.: S. road to Adelaida 6.4 mi. from its junction with Oak Flat Road, *Lewis & Thompson* 1099 (LA, RSA, UC). SANTA BARBARA CO.: 1.5 mi. W. of Juncal Campground, upper Santa Ynez Valley, 1,750 ft., B2236; 4.4 mi. E. of Santa Ynez Peak along El Camino Cielo, 3,300 ft., B2689; Tunnel Road 2.5 mi. N. of U.S. Hwy. 150, Mission Canyon, 800 ft., B1902; above Mono Debris Dam, upper Santa Ynez Velley, 1,500 ft., B2244. SANTA CLARA CO.: 1.5 mi. E. of Red Mt. near summit of Del Puerto Road, Mt. Hamilton Range, B4889; upper Arroyo del Puerto 2.4 mi. E. of junction in San Antonio Valley, R18230; summit of Loma Prieta, Santa Cruz Mts., B4675, 5011. VENTURA CO.: Cow Spring Campground, 17.6 mi. N. of Fillmore, Topatopa Mts., 3,500 ft., B2644; U.S. Hwy. 399 at turn to Rose Valley, 3,600 ft., R17499; just N. of Wheeler Gorge Guard Station, 1,950 ft., R17498; 1.2 mi. S. of Wheeler Springs, 1,400 ft., R17496A; Camp Ozena, Ozena Valley, 3,800 ft., B2436; Sespe Creek 7.6 mi. S. of Sandstone Camp, 3,700 ft., R17500.

BAJA CALIFORNIA: 10.9 mi. N. of Santo Tomás, 600 ft., R17014; Santa Catarina, *Broder* 436 (progeny = R18992, 19754).

Camissonia ignota (Jeps.) Raven (22 individuals, 18 populations), $n=7$:

U.S.: CALIFORNIA: LOS ANGELES CO.: Soledad Canyon, *Lewis* 1676 (3 plants; LA, RSA). ORANGE CO.: Lower San Juan Campground, Santa Ana Mts., W180 (SDSC). RIVERSIDE CO.: 5 mi. NW. of Alberhill, *W* in 1967 (2 plants; LA); State Hwy. 74, 1.6 mi. NE. of junction with State Hwy. 71, near Elsinore, R16914; 5.7 mi. SE. of U.S. Hwy. 395 on State Hwy. 74, road to Hemet, 1,600 ft., B1898; Reche Canyon, R17472; Dripping Springs Campground, 1,700 ft., R17385; Lake Mathews road 14.7 mi. W. of U.S. Hwy. 395, R16909. SAN DIEGO CO.: NW. of Fallbrook, W206 (SDSC); 2.3 mi. S. of Rincon Springs on road to Escondido, 1,100 ft., R17402 (progeny = R18787, 19751); 2.7 mi. SE. of Aguanga, 2,400 ft.,

R17387; Lyons Valley along road 8 mi. NE. of Jamul, 1,800 ft., R17434. SAN LUIS OBISPO CO.: 1.2 mi. S. of Santa Margarita to Simmler road on road to Navajo Camp, La Panza Range, 2,000 ft., R16970. SANTA BARBARA CO.: Juncal Campground, upper Santa Ynez Valley, 1,800 ft., B2229; S. bank of Cuyama R. on State Hwy. 166, 1.6 mi. E. of Tepusquet Canyon Road, 1,800 ft., B1930. VENTURA CO.: Boney Ridge, Santa Monica Mts., grown at Stanford, R18173.

Camissonia intermedia Raven (60 individuals, 53 populations), $n=14$:

U.S.: CALIFORNIA: CONTRA COSTA CO.: Mt. Diablo, B4698. LAKE CO.: 4 mi. W. of Reiff, R20213. LOS ANGELES CO.: Soledad Canyon, *Lewis & Thompson* 1616 (LA); near Bird Park, Memorial Canyon, Avalon, Santa Catalina I., R17857, 18171. SANTA MONICA MTS., LOS ANGELES CO.: just S. of Agoura, 850 ft., R17520; Corral Canyon, 1,900 ft., R17512 (progeny=18756); 0.9 mi. W. of Seminole Hot Springs, 800 ft., R17518; 2.6 mi. E. of Seminole Hot Springs, R17517 (type collection); Mulholland Hwy. just E. of junction with Decker Road, 1,600 ft., R17515; Stuntz Canyon Road 3.1 mi. below junction to Saddle Peak, 1,200 ft., R17511; Saddle Peak Road 0.9 mi. above Stuntz Canyon Road, 2,200 ft., R17509; Saddle Peak Road 2.4 mi. above junction of La Tuna Canyon Road, 2,400 ft., R17507; La Tuna Canyon 3.6 mi. N. of Coast Highway, 1,800 ft., R17504. MONTEREY CO.: Big Sandy Valley 2 mi. N. of Indian Valley Road, R18289; Hastings Reservation, R18220, 18218; just N. of Hastings Reservation, R18225; road to Jamesburg 0.8 mi. from main road up Carmel Valley, R18227; W. edge of San Antonio Valley, Santa Lucia Mts., 1,350 ft., B2267; 2.1 mi. SW. of Arroyo Seco Guard Station, 1,250 ft., B2305; 6 mi. W. of Priest Valley on State Hwy. 198, 2,500 ft., B2376; 0.6 mi. SW. of San Benito Co. line on road from Bitterwater to King City, R18201; The Indians, Santa Lucia Mts., R18213, 18264, 18268; Lowes Canyon, R18293, 18298. RIVERSIDE CO.: Machado Road 1 mi. SW. of U.S. Hwy. 71, W193, 194 (SDSC); 3.3 mi. W. of Dripping Springs Campground, 1,500 ft., R17382. SAN BENITO CO.: 3.7 mi. from Hernandez on road to New Idria, R15087. SAN DIEGO CO.: 2.7 mi. W. of De Luz on road to Fallbrook, 600 ft., R17483; 2.4 mi. from Fallbrook on road to De Luz, R17477 (progeny=R18758); road to Fallbrook at junction with U.S. Hwy. 395, 950 ft., R17484. SAN LUIS OBISPO CO.: 1.2 mi. W. of Bee Rock, R18305; near junction 1.8 mi. W. of Paso Robles, R18327. SANTA BARBARA CO.: Head of Buckhorn Canyon, summit of San Rafael Mts., 2,600 ft., B2779; Alamo Pintado Creek, 7–8 mi. N. of Los Olivos, Birbent Canyon, base of Figueroa Mt., ca. 1,400 ft., B2498; Little Agua Caliente Hot Springs, 1.5 mi. NE. of Mono Debris Dam, 1,700 ft., B2230; 0.9 mi. N. of State Hwy. 150 on San Roque Road, Santa Barbara, 800 ft., B2228; Portazuela Grade, Santa Cruz I., R15197; Prisoners Harbor, Santa Cruz I., R18172. STANISLAUS CO.: 12 mi. W. of Patterson on road to Mt. Hamilton, B4856. VENTURA CO.: Cow Springs Campground, 17.6 mi. N. of Fillmore on Cow Springs Road, Topatopa Mts., 3,500 ft., B2617; 0.3 mi. S. of Camp Comfort, S. of Ojai, R17493 (progeny=18755); 1.2 mi. S. of Wheeler Springs, R17496 (progeny=18768); Little Sycamore Canyon, Santa Monica Mts., *Lewis* 1666 (LA, RSA).

BAJA CALIFORNIA: 10 mi. S. of Ensenada, R17053; 15.2 km. N. of San Vicente, R12308; 5.5 km. S. of San Vicente, R17019; 19.5 km. SE. of San Vicente, R12263; 2.5 mi. S. of Ejido México, R17040; 4 km. S. of Ejido México, R12234; 11.3 mi. N. of Colonia Guerrero, R17037; 8.5 km. E. of El Rosario, R12429; Summit of Aguajito Grade, 2 km. E. of Rancho Aguajito, R12523.

Camissonia lewisii Raven (23 individuals, 19 populations), $n=7$:

U.S.: CALIFORNIA: LOS ANGELES CO.: Point Dume, W13, 170; Playa del Rey, W273. ORANGE CO.: Lower edge Cleveland National Forest, just above San Juan Guard Station, R17490 (progeny=R18764, 19079). SAN DIEGO CO.; 2.7 mi. from

Fallbrook on road to De Luz, R17478, W207; Carlsbad, R14032; Switzers Canyon, San Diego, W212; Balboa Park, San Diego, W859 (SDSC); Otay Lakes Road 1.8 mi. E. of Bonita Road, R16971.

BAJA CALIFORNIA: 2.1 mi. S. of El Descanso, *Klein & Gregory* 1186; ca. 3 mi. S. of Ensenada, *Klein & Gregory* 1273, R17011; 7.5 mi. N. of Santo Tomás, R17017, 17050; 5.5 mi. S. of San Vicente, 950 ft., R17021; 1.1 mi. N. of Colonia Guerrero, R17035 (type collection); 2 km. N. of Colonia Guerrero, R12135; San Quintín, R12362; 3 mi. S. of San Quintín, *Gregory* 335 (RSA, US); 14 mi. S. of San Quintín, R17030; 5 mi. NE. of El Rosario, *Klein & Gregory* 1266; ca. 13 mi. SE. of El Rosario, *Klein & Gregory* 1249.

Camissonia luciae Raven (7 individuals, 7 populations), $n=21$:

U.S.: CALIFORNIA: MONTEREY CO., SANTA LUCIA MTS.: Road to Jamesburg 0.8 mi. from main road up Carmel Valley, R18150; shale roadbank 7.8 mi. SW. of Arroyo Seco Guard Station on road to Jolon, B2299; Hastings Reservation, near Jamesburg, R18221; The Indians, R18267 (type collection). SAN BENITO CO.: 3.1 mi. W. of Fresno Co. line on road from Coalinga to Hernandez, *Lewis et al.* 1342–1. SANTA BARBARA CO., SAN RAFAEL MTS.: 1.3 mi. N. of Cachuma Guard Station, *Lewis* 1678 (LA); Davy Brown Campground, *Lewis* 1647 (LA).

Camissonia micrantha (Hornem. ex Spreng.) Raven (47 individuals, 39 populations), $n=7$:

U.S.: CALIFORNIA: CONTRA COSTA CO.: Antioch, R18141; 1 mi. S. of Oakley, R18143. LOS ANGELES CO.: Claremont, W271 (SDSC), R17120, 17121; Point Dume, W13 (SDSC), 171. MONTEREY CO.: Hastings Reservation, R18224; Big Sandy Valley, R18283; 3 min. N. of summit of Hog Canyon Road, S. of Parkfield, R18299; Bradley, R18307. RIVERSIDE CO.: 11 mi. W. of Riverside, *Snow & Mosquin* in 1957 (LA). SAN BENITO CO.: Pinnacles National Monument, B2183, *Lewis* 1340; 1.1 mi. S. of Cienaga School, R18198; 5.1 mi. N. of Cienaga School, R18196. SAN BERNARDINO CO.: Alta Loma, R16987. SAN DIEGO.: U.S. Hwy. 395, 2 mi. S. of turn to Lilac, R16950, 17457. SAN FRANCISCO CO.: Lake Merced, R18160. SAN LUIS OBISPO CO.: Near mouth of Arroyo de la Cruz, *Hardham* in 1963; 2 mi W. of Nipomo, B4269; 1.2 mi. N. of Simmler-Creston road on road to Shandon, R16972, 18321; near Atascadero, R18277; 1.8 mi. W. of Bee Rock, R18034; 2.9 mi. E. of San Miguel, R18310; 1.2 mi. E. of Santa Margarita, R18312, 3.8 mi. E., B2026, 3 mi. E., R18314, 3.7 mi. NE., R18316, 4.2 mi. NE., R18317, 18.6 mi. NE., R18319, 18320; Nipomo Valley 1.5 mi. N. of Santa Barbara Co. line, R16955; S. road to Adelaida 6.4 mi. W. of junction with Oak Flat Road, near Paso Robles, *Lewis & Thompson* 1100 (LA). SANTA BARBARA CO.: 1 mi. W. of Goleta, B1967; Jalama Beach, R14039; 4 mi. N. of Lompoc, R15510; 1.7 mi. N. of Santa Ynez R. on State Hwy. 1, B2556; San Miguel I., R18178; Cherry Canyon, Santa Rosa I., R14962. SANTA CRUZ CO.: Sunset Beach, R18187; near Ben Lomond, R18183, B4637. SONOMA CO.: Bodega Bay, R18245.

CULTIVATED: Seeds from Copenhagen Botanic Garden as *Oenothera hirta*, R18242.

Camissonia pallida (Abrams) Raven subsp. **hallii** (Davids.) Raven (4 individuals, 3 populations), $n=7$:

U.S.: CALIFORNIA: RIVERSIDE CO.: Jumbo Rocks Campground, Joshua Tree National Monument, R17116; Whitewater Canyon 2.7 mi. from U.S. Hwy. 70–99, R17109; Morongo Canyon, *Lewis* 1682 (LA, RSA); Morongo Canyon, ca. 8 mi. from U.S. Hwy. 60–70–999, W231 (SDSC).

Camissonia pallida subsp. **pallida** (26 individuals, 24 populations), $n=7$:

U.S.: ARIZONA: MOHAVE CO.: 9 mi. N. of Kingman, 2,950 ft., R17359. YAVAPAI CO.: 5.4 mi. NE. of Congress, R18367 (progeny = R18767, 19752).

U.S.: CALIFORNIA: KERN CO.: Kern R. 6 mi. S. of Roads End P.O., 3,100 ft., *Howell* 33144 (progeny = R19081, 19747); W. of the mouth of Kern R. Canyon, *Lewis* 1670 (LA, RSA). LOS ANGELES CO.: Big Rock Creek, San Gabriel Mts. R11961; 0.5 mi. N. of Pearblossom, 2,800 ft., R17104; 0.2 mi. E. of Pearblossom, *Lewis & Wedberg* 1692 (LA); 1 mi. W. of Littlerock, R13995. RIVERSIDE CO.: Whitewater Canyon, *W* in 1957 (LA); near San Bernardino Co. line in Morongo Canyon, W232; Pinyon Crest Road 2.5 mi. from Palms-to-Pines Hwy., *Theobald* 62. SAN BERNARDINO CO.: Cushenbury Grade 0.5 mi. below Cactus Flat, San Bernardino Mts., 5,900 ft., R17461; Bonanza King Mine, Providence Mts., R17358 (progeny = R18769, 19753). SAN DIEGO CO.: 8.7 mi. S. of Scissors Crossing on road to Vallecito Valley, R16902, 9.1 mi. SE., R11536, 6.8 mi. S., R16900; San Felipe Creek wash 2 mi. E. of road to Yaqui Pass, R16895, 2.2 mi. W. of road W219 (SDSC), in 1957 (LA); Vallecito Valley just outside Anza-Borrego State Park boundary, R16904; N. end of Vallecito Valley, W222; 0.8 mi. E. of Banner Queen Store, Banner Grade, R16923; 2.5 mi. inside Anza-Borrego State Park on road from Scissors Crossing, W221; 3 mi. from Banner on road to Borrego Valley, W216 (SDSC); Ensign Ranch, Borrego Valley, *H. & M. Lewis* 1637A (LA), 1637B (LA).

Camissonia proavita Raven (4 individuals, 4 populations), $n=7$:

BAJA CALIFORNIA: 5.5 mi. S. of San Vicente, R17020 (type collection); 19.5 km. SE. of San Vicente, R12264; 1.2 mi. N. of Colonia Guerrero, R17034; San Quintín, R12363.

Camissonia robusta Raven (29 individuals, 24 populations), n = 21:

U.S.: CALIFORNIA: LOS ANGELES CO.: SANTA CATALINA I.: Haypress, R17807 (progeny = 18170). SAN CLEMENTE I.: *Piehl* 62387 (progeny = R18174). SAN DIEGO CO.: U.S. Hwy. 395, 2 mi. S. of turn to Lilac, R17458 (progeny = 18846); 4.8 mi. W. of Pala, R17061; 1.6 mi. E. of Pala, R16921, 17062; 4.6 mi. E. of San Pasqual, R17407; 2.3 mi. E. of Ramona, R17411; 0.3 mi. from U.S. Hwy. 395 on Deer Springs Road to San Marcos, R17474; 0.7 mi. N. of Felecita County Park, R17453; Balboa Park, San Diego, W214 (SDSC); Sweetwater Road, San Diego, W860 (SDSC); Descanso to Lyons Valley road 3.2 mi. NE. of turn to Camp Barrett, R17431; 2 mi. E. of Chula Vista on road to Bonita, B1809; Barrett, R16937 (3 plants). SANTA BARBARA CO., SANTA CRUZ I.: Top of Ridge between Coches Prietos Canyon and Alberts Anchorage, 400 ft., *Blakley* 3314 (progeny = R18756, 19077).

BAJA CALIFORNIA: Above La Misión, between Tijuana and Ensenada, R17056; 10 mi. S. of Ensenada, R17054; ca. 16 mi. S. of Ensenada, *Klein & Gregory* 1195; 10.9 mi. N. of Santo Tomás, R17012; 7.5 mi. N. of Santo Tomás, R17016, 17051A; 5.5 mi. S. of San Vicente, R17022 (2 plants); 7.4 mi. N. of Ejido México, 500 ft., R17043. GUADALUPE I.: NE. side of Barracks Cove Canyon, *Copp* 151 (progeny = R18759); Northeast Anchorage, *Wiggins & Ernst* 222 (progeny = R18754, 19078).

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BREDIN-ARCHBOLD-SMITHSONIAN BIOLOGICAL SURVEY OF DOMINICA

Myxomycetes from Dominica

By MARIE L. FARR

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BREDIN-ARCHBOLD-SMITHSONIAN BIOLOGICAL SURVEY OF DOMINICA

Myxomycetes from Dominica [1]

By MARIE L. FARR [2]

Introduction

This paper is based mostly on the collections made during my participation in the Bredin-Archbold-Smithsonian Biological Survey of Dominica (British West Indies). Species of myxomycetes previously reported from this island but not found on this expedition are also included to bring the record up to date. The present report although based on a very short collecting period and, therefore, far from complete, evidently represents the first extensive investigation of the slime molds of Dominica.

From January through March 1966, over 500 myxomycete specimens were collected in the field and 63 were obtained from 187 moist chamber cultures. These efforts yielded 96 taxa (1 doubtful) of which 2, 1 of *Diachea* and 1 of *Physarum*, are described here as new species.

Dominica, the largest of the Windward Islands and third largest of the Lesser Antilles, is located at 15°10′–15°40′ N. latitude and 61°44′–61°30′ W. longitude, about halfway between Guadeloupe and Martinique, and has an area of slightly more than 300 square miles; its maximum length is ca. 29 miles and its greatest width, ca. 15 miles. The highest peaks are Morne Diablotins (ca. 4,700 ft.), Morne Trois Pitons (ca. 4,500 ft.), Watt Mountain (ca. 4,000 ft.), and Morne Micotrin (ca. 3,900 ft.). Because of its relatively recent volcanic origin, the island is characterized by a much craggier topography and a (consequently) wetter climate than other major Caribbean Islands. The difficulties in road building, timber harvesting, etc., caused by the rugged terrain; the heavy downpours; and the strong

[1] This is the first in a series of floristic studies. Other floral papers in this series will appear in "Smithsonian Contributions to Botany." A companion series on the fauna appears in the "Proceedings of the United States National Museum" and "Smithsonian Contributions to Zoology."

[2] Mycologist, Crops Research Division, Agricultural Research Service, U.S. Department of Agriculture, Beltsville, Maryland 20705.

winds have retarded the advancement of lumbering, agriculture (less than half of Dominica was under cultivation in 1963), and tourism, and have resulted in the preservation of relatively large tracts of the typical Caribbean forests that have largely disappeared from the more highly developed islands. The last decade or so, however, has witnessed an acceleration in road construction and the erection of an airport, which, among other factors, are greatly hastening the conversion of virgin lands to crop cultivation and the development of tourist trade and facilities.

Unpublished climate maps [3] show that only a very narrow coastal fringe (mostly less than 2 miles wide) receives less than 100 inches of yearly rainfall and experiences a true dry season; most of the mountainous interior lies in the zone characterized by 200–300 inches, or even more. The relative humidity is always high (50–80% in Roseau, 85% or more in the interior) and a considerable amount of precipitation occurs even during the drier parts of the year. The temperature range is ca. 65–90° F., averaging in the upper seventies. According to Hodge (16), from whose extensive treatise much of the present introductory information was taken, a dry season extends from mid-January to mid-June, April being the driest and calmest month. The wet season consists of a summer portion (mid-June to mid-September), a "break" of "complete sunny days with occasional heavy showers only at night" (mid-September to mid-November), and a winter portion (mid-November to mid-January). Fentem (12) mentions an "undependable and indefinite drought between mid-January and mid-June on the leeward coast which generally lasts about 6 weeks" and a tendency toward a second period of minimum rainfall in September and October.

In view of the generally high precipitation and humidity one would imagine the dry season to be the best time on most parts of the island for gathering myxomycetes. Enough moisture is present, even then, for their development, yet fructifications can ripen completely without being washed away immediately by intense downpours or rapidly disfigured by filamentous molds. The validity of this assumption remains to be tested by collecting in Dominica during the wet season. Certain areas subjected to pronounced droughts, however, may be expected to produce myxomycetes only after the onset of rainy periods. In Jamaica, for example, certain pastured and wooded tracts exhibiting distinct seasonal changes in verdure were myxomycologically barren during the dry season, but very fruitful during or immediately following the rainy season (9).

Most of my time on Dominica supposedly coincided with the "dry" season, but the weather was somewhat different from that anticipated.

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[3] Kindly supplied by the Lands & Surveys Department of Dominica.

An unusually dry spell in December and January, which sometimes necessitated a partial curtailment of electric power, but provided very pleasant weather, was followed by an extremely wet February and an only slightly drier March. February, especially, was marked by nightly violent downpours changing into milder, more or less intermittent rain of varying intensity nearly every day (at least, inland). Although the nearly continuous rain impeded slime-mold collecting considerably, my dampened spirits were revived by the discovery of a number of myxomycetes fruiting in good condition, even during the rain, in certain rather sheltered niches; the undersides of very large logs, and substrates protected by "umbrellas" of overlapping banana leaves or buried within piles of leaf litter, yielded collections of several species.

Topographic and climatic features of the island have given rise to a diversity of soil types and microenvironments, resulting in a corresponding distribution of vegetation types. Hodge (16) lists the following five primary plant formations, of which all but the first are climatic: 1. Swamp forest, an edaphic climax occurring only in a few small places on the island and represented in my collections by locality no. **14.** 2. Dry evergreen formation, including the littoral woodland vegetation of the windward (E.) coast. 3. Seasonal formations, such as the thorny scrub vegetation along the dry leeward (W.) coast and more or less evergreen forests in other areas exposed to periodic drought; this formation has been largely replaced by crop cultivation. 4. Rain forest, the dominant, luxurious vegetation type of the wet interior regions, much of which has become secondary or suboptimal as a result of encroachment by shifting agriculture. Partially cleared areas, in which considerable decay of stumps and felled trees has already taken place, usually offer great promise for the collector. The accumulation of rotten logs and other plant debris, the presence of living crop plants (the most common substrate for some slime molds), the more open, sunny situations created by removal of the forest, and the surrounding border of undisturbed, shaded woodland provide a variety of habitats and microenvironments and a corresponding diversity of myxomycete species. This type of situation is represented in my collections by localities **7–12,** of which no. **8** yielded the greatest number of species. The undisturbed rain forests of the mountain slopes, on the other hand (except for locality no. **13**), generally were found to be relatively unproductive despite the seemingly ideal combination of high moisture, deep shade with sporadic, moderate sunlight, windstillness, and abundance of rotten wood. (Rather surprisingly, however, several myxomycetes developed in bark cultures of the strongly resinous codominant tree, "gommier" [*Dacryodes excelsa* Vahl.].) The paucity of myxomycetes, which seems to prevail in this type of habitat in other Caribbean islands as well, has puzzled

collectors for some time. Possibly the substrates are too acid to permit spore germination or subsequent development of many species. The density of the vegetation and the relative lack of air movement could be expected to retard spore dispersal within the forest. Most wood-inhabiting animals that might feed on myxomycetes were comparatively uncommon in the deep forest and can probably be ruled out as cause of the sparse myxomycota. 5. Montane formations, found on mountain summits and similar habitats exposed to strong, desiccating winds, and consequently characterized by stunted vegetation types such as "elfin woodland." These are unproductive for field collecting of slime molds. Two rather poor but interesting moist chamber developments (*Physarum ?leucopus* and *P. ?bubalinum*) were obtained from plant material collected at the top of Morne Diablotins. One would surmise that great numbers of spores would be deposited in such an open habitat, and that the cooler temperatures of the summits might permit the survival of some species not normally thriving in the tropics. Extensive collecting of substrate samples from this formation, followed by moist chamber culture, would be a worthwhile undertaking for energetic collectors possessing the endurance to make repeated climbs to the summits and the stamina to collect after reaching them.[4]

Politically, Dominica is divided into 10 parishes of greatly differing size; the largest ones are St. Joseph on the west side, St. David on the east side, and St. Andrew to the north and northeast. Most myxomycete collecting was carried out in these, as well as in St. Paul and St. George, mainly because of accessibility. Although these parishes proved highly fertile, some of the others may, upon thorough exploration, turn out to be at least equally rich in myxomycetes.

Slime molds (including field collections and moist chamber fruitings) were acquired from about three dozen localities, of which (to save space) the 16 represented by the greatest number of field specimens are coded by number and pinpointed on map 1. The first 10 constituted more or less "favorite" collecting spots because of their combined accessibility and high yield (mostly more than 20 specimens). Nos. **11–16,** lower in yield, appeared very promising but, owing to distance or inaccessibility, were less frequently and thoroughly searched for myxomycetes. Nos. **1–3** are in St. Joseph; **11–12** in St. Peter; **4** in St. John; **5**, **13**, and **14** in St. Andrew; **6**, **8**, **15**, and **16** in St. David; **9** in St. George; **7** and **10** in St. Paul. They are briefly described in the following paragraphs. The absence of road numbers or names, and of accurately defined or permanent landmarks, accounts for the sometimes awkward citations of locality.

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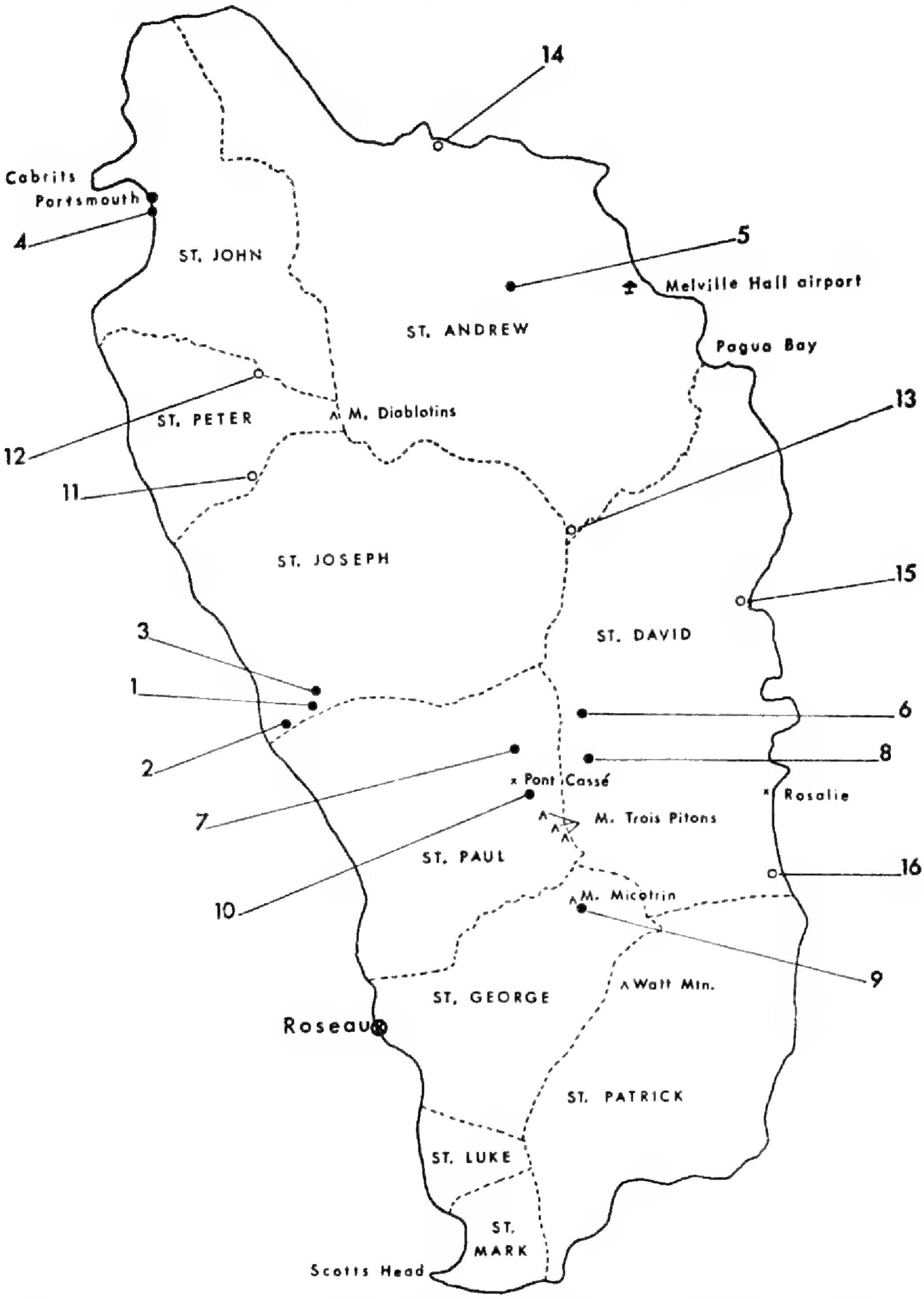
[4] On certain other islands, well-established footpaths to the mountain summits make this habitat more easily accessible than it is, at present, in Dominica.



Map 1.—Dominica, B.W.I., showing the 16 most productive collecting localities for myxomycetes.

1. St. Joseph: Clarke Hall Estate and vicinity (ca. half-mile radius), along the Layou River (the largest river on the island), extending E. approximately to the swinging footbridge and SE. to the "Café" area, elev. 100–200 ft. This region, traversed by one of the major roads, is almost entirely cultivated and most of the gatherings

were made in old, well-established cacao, banana, or coconut plantations between highway and river, or along the roadside.

2. St. Joseph: From Clarke Hall W. to the highway bridge near the mouth of the Layou River, elev. ca. 150 ft. to nearly sea level, an area essentially similar to no. **1**.

3. St. Joseph: Mannetts Gutter, a small creek (marked but not labeled on current maps) ca. ½-mile NE. of Clarke Hall, continuing N. from the road passing Brookhill Estate, elev. ca. 200 ft. Most myxomycetes were collected on large, more or less shaded, wet, rotten logs and surrounding plants and debris near an ascending footpath along the W. bank of the creek.

4. St. John: S. of Portsmouth, near the mouth of the Indian River, elevation near sea level, a dry area (at least when visited) on the leeward (W.) coast. The species found, predominantly those tolerant of some exposure (*Lycogala epidendrum*, the common *Hemitrichia* spp., *Stemonitis webberi*, etc.), were collected mostly on relatively dry, more or less shaded logs in open areas.

5. St. Andrew: Governor Estate, 3-4 miles W. of the airport, and also beyond the end of the jeep road on a footpath ascending into the disturbed rain forest, elev. ca. 400-600 ft. Myxomycetes were picked up on the estate itself in low-lying plantations next to the Clyde River, as well as along the forest path.

6. St. David: St. David Bay road, ca. 1.5 miles N. of its intersection with Rosalie road, near L'Arouma Popotte, elev. ca. 1,000 ft. Slime molds were collected mostly in clearings and banana plantations adjoining the highway, on rotting logs and in leaf litter.

7. St. Paul: 1-2 miles N. of Pont Cassé, in banana plantations on the E. side of the highway leading to the airport, elev. 1,350–1,450 ft., habitat and substrates essentially similar to those of locality no. **6**. Collecting efforts on the W. side of the road were unrewarding, probably because those plantations were experimental plots for poisonous chemicals.

8. St. David: About 100 yards E. of the intersection between the roads to St. David Bay and Rosalie, along the latter, elev. ca. 1,400 ft. This locality, reached by a short, narrow, steep footpath descending from a roadside parking area, was characterized by an ideal diversity of habitats, consisting of a dense, secondary rain forest encircling a newly cut, sunny clearing next to a slightly older one planted to banana trees and root crops; the entire cut area was lined with numerous large logs (many of which were covered with moss, filmy ferns, and various other epiphytes) and stumps from the original forest in various stages of decay. Of all stations visited, this spot proved the richest in number of species, but its productivity declined rather sharply during the last month or so of my stay.

9. St. George: Along the road between Laudat and Fresh Water Lake, and on the basal S. slope of Morne Micotrin, elev. ca. 2,400 ft. Usable by passenger cars nearly all the way, this is the highest paved road on the island and cuts through the rich montane rain forest of Morne Micotrin; thus, botanists find many species typical of this plant formation by merely hiking along the road or making short forays into the forest. The average annual rainfall measured at a weather station near the lake is about 250 inches. Most of the myxomycetes were collected near the road (at the edge of the forest) and in adjacent citrus orchards.

10. St. Paul: Along the basal part of the trail ascending Morne Trois Pitons on its NW. slope, near Pont Cassé, elev. 2,000–2,200 ft., a region of disturbed montane rain forest grading into newly cut clearings and banana plantations.

11. St. Peter: Rochette, ca. 2-3 miles inland from Colihaut, elev. 2,200 ft., also an area of disturbed rain forest and cultivation.

12. St. Peter (border of St. John): S. end of Syndicate Estate, near the road junction and on the basal slope of Morne Diablotins, elev. 2,000–2,100 ft., an area of more or less disturbed rain forest merging with banana and citrus plantations. Myxomycetes were collected mostly in the forest.

13. St. Andrew: Central Forest Reserve, Borne area, elev. ca. 1,400 ft., in rain forest.

14. St. Andrew: Near the road junction ca. 1.5 miles W. of Eden Estate, in the swamp-woodland formation by the Eden River (probably the spot cited by Hodge as 2 miles W. of Calibishie). Myxomycetes were found on a group of huge *Pterocarpus officinalis* Jacq. logs lying in the swamp-woodland, on decaying logs on solid ground across the road, or were cultured from bark of nearby *Terminalia catappa* L. and *Carica papaya* L. trees.

15. St. David: Near the road bridge by the mouth of the Castle Bruce River, elevation near sea level; a dry (at least when visited), flat coastal area partly planted to coconut and banana.

16. St. David: Taberi Estate, near the mouth of the Bibiay River, elev. 150-200 ft., essentially similar to locality no. **15**.

Certain places, such as Felicite (St. Patrick) and South Chiltern House (St. Luke) were infertile with respect to field collections but brought forth a good number of specimens from bark samples in moist chamber culture, denoting a potential productivity.

In addition to the field collections, nearly 200 moist chamber cultures were maintained during the 3 months. They contained mostly pieces of bark from living trees, but occasionally also deadwood from the beach, various types of plant detritus, pieces of burlap, sclerotia, and living plasmodia with pieces of their substrates. The cultures

were prepared usually the same day as collected by soaking the samples (except active plasmodia) overnight in new, stacked finger bowls that had been washed in tap water, covered on the bottom with filter paper, and filled with tap water to cover the sample. After the excess water was poured off, the dishes were observed every few days for myxomycete developments and substrate pieces bearing ripe fructifications were removed. Since the only purpose of this work was to supply further records of species occurring in Dominica, no attempt at sterilization of the cultures was made. The use of new materials and the performance of the entire work on the island rendered foreign contamination unlikely. The cultures were kept at least one month and those not disintegrated or overrun by filamentous molds were again soaked overnight and maintained approximately another month; no effort was made, however, to provide a uniform timetable for all cultures. The rewetting procedure added an unexpectedly large number of specimens, bringing the proportion of moist chambers producing myxomycetes to ca. 35%.

Geographical Considerations

The present known total for Dominica of 99 or 100 species of myxomycetes compares very favorably with approximate figures published for other Caribbean islands (Antigua, 50; Cuba, 24, Hispaniola, 30; Jamaica, 110; Puerto Rico and Virgin Islands, 70; Trinidad, 50) and indicates that this verdant island abounds in slime molds. In addition to the 2 newly described taxa, 9 known species appear to constitute new records for the Antilles: *Cribraria minutissima, Licea operculata, Perichaena minor, Comatricha subcaespitosa, Echinostelium cribrarioides, Diderma chondrioderma, Didymium comatum, Physarum psittacinum,* and *P. pulcherripes*. Especially interesting among these is *Echinostelium cribrarioides,* previously noted only from the Greek type collection. *Badhamia panicea*, an early record (17), is still known, in the West Indies, only from Dominica.

Table 1 shows several other species to be noted from only one additional Caribbean island (*Ceratiomyxa sphaerosperma, Hemitrichia paragoga, Comatricha aequalis, Macbrideola martinii, Stemonitis flavogenita, Badhamia affinis, Didymium intermedium, Physarum galbeum, P. roseum,* and *P. rubiginosum* from Jamaica; *Perichaena vermicularis* and *Didymium minus* from Antigua; *Didymium crustaceum* from Cuba; *Badhamia nitens* and *Didymium difforme* from Hispaniola; and *Physarum auriscalpium* from St. John, U.S. Virgin Islands). These listings, however, probably do not reflect the actual Antillean distributions for the species concerned, because the myxomycota of most of the islands has not yet been intensively surveyed. Floristic

studies of the myxomycetes inhabiting the Caribbean islands are still in the beginning stages.

A number of species more or less common in the West Indies were not encountered in Dominica, but are undoubtedly present and perhaps prevalent during some other time of the year. *Badhamia nitens*, *B. panicea*, *Stemonitis herbatica*, and *Diderma rugosum*, reported by Lister (17), were not recovered; *Arcyria nutans* and *Comatricha nigra* were conspicuous by their absence; *Arcyria insignis* and *Diderma testaceum* likewise will probably be added to the record by future collectors. As might be expected, *Ceratiomyxa fruticulosa*, *Arcyria cinerea*, *A. denudata*, *Hemitrichia stipitata*, *H. vesparium*, *H. serpula*, *Stemonitis fusca*, *Fuligo septica*, and *Physarum melleum* were practically ubiquitous throughout the collecting period. *H. stipitata*, as in Jamaica and elsewhere, fruited under widely differing conditions of moisture and exposure, its habitat ranging from dry, burnt, exposed wood to very wet, rotten, deeply shaded logs. *Cribraria violacea* (in moist chamber), *Diderma effusum*, *Didymium nigripes*, *D. squamulosum*, *Physarum compressum*, *P. nucleatum*, and, oddly, *Trichia favoginea* (a temperate-zone species not very often collected in the tropics) likewise showed up frequently. *Lycogala epidendrum* was abundant, but *L. exiguum* was almost equally common. *Tubifera microsperma*, *Comatricha typhoides*, *Clastoderma debaryanum*, and *Physarum nutans* were not as prevalent as in Jamaica, but *Didymium squamulosum* was by far more plentiful in Dominica.

Lister (18) remarked on the scarcity of the genus *Trichia* in Antigua and speculatively attributed its [then] absence in Dominica to the rapid destruction, by termites, of rotten wood, which is the substrate for plasmodia of *Trichia* spp. This reasoning seems unfeasible, since other wood-inhabiting slime molds (*Hemitrichia* spp., *Stemonitis* spp., *Lycogala* spp., etc.) were then known from Antigua and are widely distributed over the Caribbean region. In Jamaica 8 species of *Trichia* are known, but there the genus is generally confined to the higher altitudes (4,000 ft. or more) having a more temperate climate. The more tropical environment and absence of such high elevations on Antigua and (except on a few windswept peaks) Dominica may provide a more plausible explanation. *Trichia favoginea*, however, is well established on the latter island, and additional species of *Trichia* may well develop at other times of the year.

One disappointing surprise was the lack of myxomycetes on or within the abundant epiphytic bromeliads, a habitat frequently colonized by certain species in Jamaica.

Obviously a minimum of one year's study would be required to gain even a preliminary knowledge regarding any seasonal distribution of the various slime-mold species on Dominica. Since the short

TABLE 1.—*Hitherto known Antillean distribution of myxomycetes collected in Dominica*

Species	Antigua	Cuba	Dominica	Guadeloupe	Hispaniola	Jamaica	Martinique	Puerto Rico and U.S. Virgin Islands	Trinidad	References
Ceratiomyxales										
Ceratiomyxa fruticulosa	X		X	X	X	X		X	X	2, 4, 7, 8, 9, 11, 14, 17
C. sphaerosperma						X				2, 9
Liceales										
Cribraria intricata						X		X	X	4, 9, 14
C. languescens	X					X		X	X	4, 9, 14, 17
C. microcarpa						X		X		2, 9, 14
C. minutissima										New Antillean record
C. tenella	X		X			X				2, 9, 17
C. violacea	X					X		X	X	2, 4, 9, 14, 17
Dictydium cancellatum	X			X		X		X	X	2, 4, 8, 9, 14, 17
Licea operculata										New Antillean record
Lycogala epidendrum	X	X		X	X	X		X	X	4, 5, 6, 7, 8, 9, 14, 17
L. exiguum				X		X	X			8, 9
Reticularia lycoperdon						X		X		9, 14
Tubifera ferruginosa				X	X	X		X		7, 9, 11, 14
T. microsperma	X	X		X		X			X	4, 5, 8, 9, 17
Trichiales										
Arcyria cinerea	X	X		X	X	X		X	X	2, 4, 5, 6, 7, 8, 9, 11, 13, 14, 17, 21
A. denudata	X	BPI	X	X	X	X	X	X	X	2, 4, 7, 9, 11, 14, 17
A. incarnata	X				X	X		X	X	4, 9, 11, 14, 17
Hemitrichia paragoga						X				9
H. serpula	X	X		X	X	X		X	X	2, 4, 5, 7, 8, 9, 14, 17
H. stipitata	X	X		X	X	X		X	X	2, 4, 5[a], 6, 8[a], 9, 11, 13, 14[a], 17[a]
H. vesparium	X	X				X		X	X	2, 4, 5, 9, 14, 17
Perichaena chrysosperma	X	X			X	X		X	X	2, 4, 5, 7, 9, 11, 14, 17
P. depressa	X					X		X	X	2, 4, 9, 14, 17
P. minor										New Antillean record
P. vermicularis	X									17
Trichia favoginea		BPI [c]			X	X		X	X	2, 4[b], 7[b], 9, 14[c]
Echinostteliales										
Echinostelium cribrarioides										New Antillean record
E. minutum						X			X	2, 4, 9
Stemonitales										
Clastoderma debaryanum						X			X	2, 4, 9
Comatricha aequalis						X				9
C. elegans		BPI		X	X	X			X	2, 4, 9, 11
C. irregularis						X		X		9, 14
C. longa	X					X		X	X	4, 9, 14, 17
C. subcaespitosa										New Antillean record
C. typhoides	X	X		X	X	X		X	X	2, 4, 5, 7, 9, 14, 17
Diachea bulbillosa						X		X		9, 14
D. leucopodia	X	X				X		X	X	2, 4, 5, 9, 11, 17
D. silvaepluvialis										New Antillean record (new species)
Lamproderma arcyrionema	X				X	X		X		2, 7, 9, 11, 14, 17
L. scintillans	X				X	X				9, 11, 17
Macbrideola martinii						X				2, 3
Stemonitis axifera		X		X	X	X	X			5, 6, 7, 8, 9, 11, 13
S. smithii						X			X	4, 9
S. flavogenita						X				9
S. fusca	X	X		X	X	X	X	X	X	4, 5, 7, 8, 9, 14, 17
S. herbatica			X	X	X	X		X		6, 7, 8, 9, 14, 17, 21
S. hyperopta						X		X		9, 14
S. nigrescens						X		X		2, 9, 14
S. splendens	X					X		X	X	4, 9, 14, 17
S. webberi		X				X				9, 20

See footnotes at end of table.

TABLE 1.—*Hitherto known Antillean distribution of myxomycetes collected in Dominica*—Continued

Species	Antigua	Cuba	Dominica	Guadeloupe	Hispaniola	Jamaica	Martinique	Puerto Rico and U.S. Virgin Islands	Trinidad	References
Physarales										
Badhamia affinis					X					9
B. nitens			X	X						7, 17
B. panicea			X							17
Craterium aureum				X	X		X			6, 7, 9, 14
C. leucocephalum	X	X			X		X	X		4, 5, 9, 14, 17
Diderma chondrioderma										New Antillean record
D. effusum	X				X		X	X		4, 9, 14, 18
D. hemisphaericum	X			X	X		X	X		4, 9, 11, 14, 17
D. *rugosum*			X		X			X		4, 9, 17
D. spumarioides	X				X		X			9, 14, 17
Didymium clavus	X			X	X			X		2, 4, 9, 11, 17
D. comatum										New Antillean record
D. crustaceum		X								5
D. difforme				X						9
D. intermedium					X					2, 9
D. iridis	X			X	X			X		4, 6, 9, 11, 17, 21
D. minus	X									18
D. nigripes	X			X	X		X	X		2, 4, 7, 9, 11, 14, 18
D. squamulosum	X	X		X	X		X	X		4, 5, 7, 9, 11, 14, 17
Fuligo cinerea	X				X					9, 17
F. septica	X	X		X	X	X	X	X		4, 5, 7, 8, 9, 14, 17
Physarella oblonga	X				X		X	X		2, 4, 9, 14, 17
Physarum aeneum			X				X			14, 17
P. auriscalpium							X			9
P. bogoriense	X				X		X	X		2, 4, 9, 14, 17
P. bubalinum										New Antillean record (new species)
P. cinereum	X	X			X	X		X	X	4, 5, 7, 9, 11, 14, 17
P. compressum	X				X	X		X		6, 7, 9, 11, 14, 17, 21
P. didermoides					X	X		X		6, 7, 9, 14, 21
P. echinosporum	X					X				9, 20
P. galbeum						X				9
P. lateritium	X					X				9, 18
P. leucophaeum	X			X	X	X				2, 6, 7, 8, 9, 13, 17
P. leucopus						X				9
P. melleum	X				X	X		X	X	4, 7, 9, 11, 14, 17
P. notabile				X		X				8, 9
P. nucleatum	X					X				2, 9, 18
P. nutans					X	X		X	X	4, 7, 9, 13, 14
P. oblatum						X				9
P. penetrale						X				9
P. polycephalum		X				X		X	X	4, 5, 9, 14
P. psittacinum										New Antillean record
P. pulcherripes										New Antillean record
P. pusillum	X				X	X		X		2, 7, 9, 11, 14, 17
P. roseum						X				9
P. rubiginosum						X				9
P. stellatum	X		X			X		X	X	2, 4, 9, 14, 17
P. tenerum	X					X		X	X	4, 9, 14, 17
P. viride	X			X		X		X	X	2, 4, 8, 9, 14, 17

[a] As *H. clavata; H. stipitata* was formerly a synonym of *H. clavata* and, as indicated by Martin (20, p. 58), early tropical collections so cited were *H. stipitata.*

[b] As *T. affinis.*

[c] As *T. persimilis; T. favoginea, T. affinis,* and *T. persimilis* were united recently (10).

collecting period encompassed only ±1 season and a limited number of localities (many of which could not be visited regularly), no meaningful statements on this subject can be made at this time. However, the number and monthly distribution of collections of each species, listed in table 2, may be of interest and serve future collectors as a basis for comparison. It should be pointed out that the progressive decrease revealed by *Ceratiomyxa fruticulosa*, *Arcyria cinerea*, *A. denudata*, *Hemitrichia serpula*, *H. stipitata*, *H. vesparium*, *Didymium nigripes*, and *Physarum compressum* may be due largely to change in collecting habits rather than season. After the first month or so of collecting, these ubiquitous species were frequently passed over, except as locality vouchers or otherwise especially desirable specimens. Similarly, the more or less pronounced increase in frequency of the *Lamproderma* spp., *Diderma hemisphaericum*, *Didymium squamulosum* *Physarum aeneum*, and *P. melleum* can perhaps be ascribed, at least partly, to the fact that their preferred habitat (buried in leaf litter) was less thoroughly investigated during the first few weeks.

The number of myxomycetes acquired from moist chambers is high compared with results obtained previously in Jamaica by Alexopoulos and Beneke (2) and by me (9). More than one-third of the cultures produced myxomycetes and many yielded more than 1 species, especially after being resoaked. The often heavy infestation of the cultures with mites, springtails, etc., may have suppressed the appearance of additional species.

The development time of each of the 26 species obtained from moist chamber culture (not including those collected as plasmodia, which are considered field collections) is included in table 2; 14 of these species were also found in the field, including nearly all cited members of the Physarales. *Cribraria violacea* was the species most frequently harvested, appearing in more than a dozen moist chambers; it was, surprisingly, never observed in the field. No previously published notices of moist chamber fruitings were found for the following species: *Diderma hemisphaericum*, *Fuligo cinerea*, *Physarum leucophaeum*, *P. leucopus*, *P. melleum*, *P. notabile*, and *P. viride*.

The relatively long time needed by all myxomycetes to fruit in the moist chambers is noteworthy and perhaps due, at least partly, to the use of tap water (distilled water being unavailable). Even members of such genera as *Cribraria*, *Licea*, and *Echinostelium*, which often fruit within a few days (1), required at least 1 to 2 weeks. In the cases of *Arcyria cinerea*, *Hemitrichia vesparium*, *Lamproderma arcyrionema*, and *Physarum pusillum*, the disparity of development periods shown by different cultures within the species is perplexing, but the later fruitings (as well as some of the other species appearing after very long incubation) may have resulted from contamination during handling and rewetting.

Acknowledgments

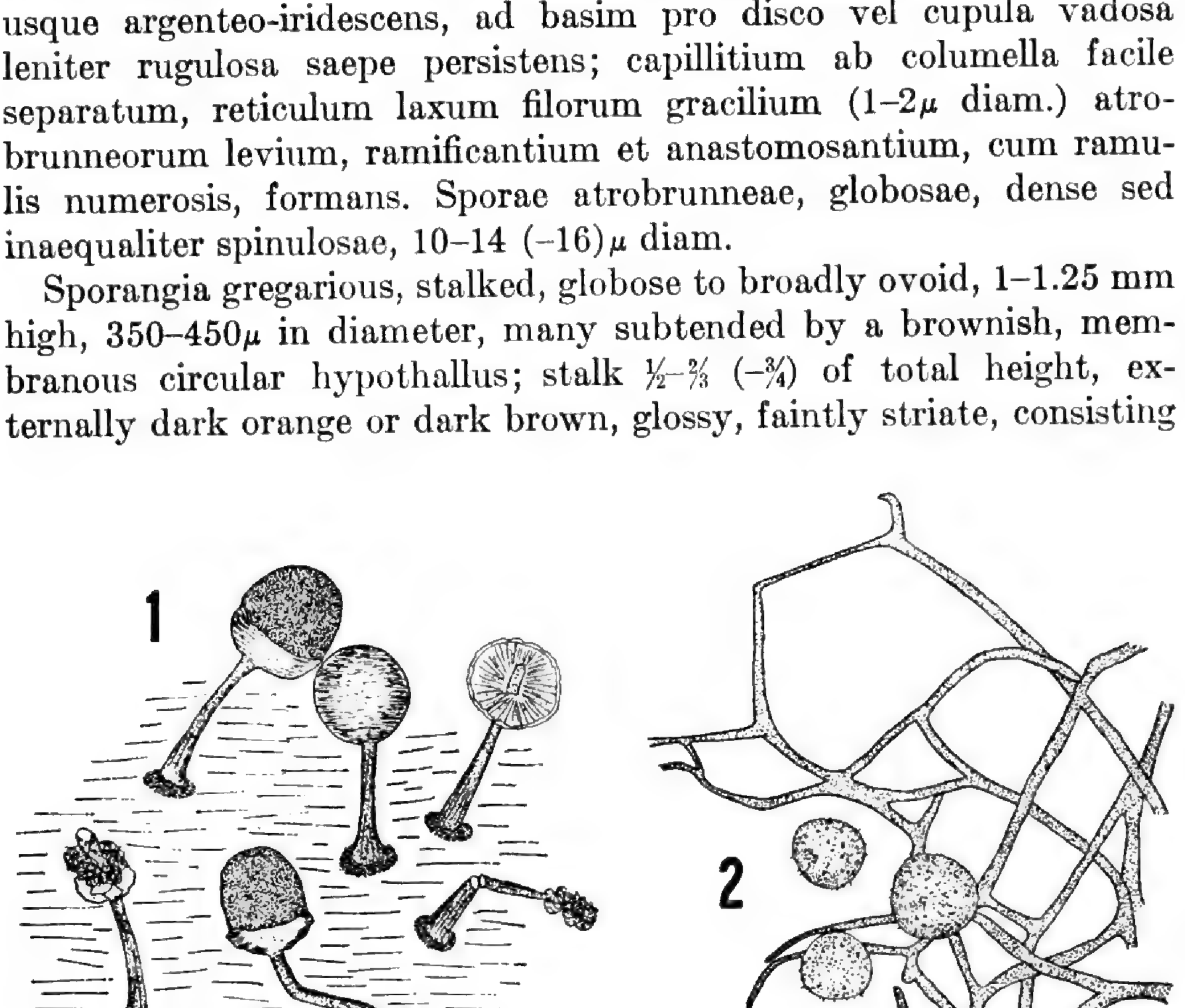
I wish to thank G. W. Martin and C. J. Alexopoulos for their help in the identification of specimens, J. A. Stevenson and P. L. Lentz for determining fungal substrates of certain collections, and Arlene Frank for technical assistance.

New Species

Diachea silvaepluvialis, sp. nov. FIGURES 1, 2

Sporangia gregaria, stipitata, globosa vel late ovoidea, 1–1.25 mm alta, 350–450μ diam., hypothallo circulari, membranaceo, brunneo plerumque subtenta; stipes 500–670 (–750)μ altus, membrana brunnea translucenti tectus, crystallis calcareis, albis 5–15μ diam. dense farctus, basaliter dilatatus, apicaliter pro columella plus minusque cylindracea apicem sporangii attingens. Peridium tenue, plus minusque argenteo-iridescens, ad basim pro disco vel cupula vadosa leniter rugulosa saepe persistens; capillitium ab columella facile separatum, reticulum laxum filorum gracilium (1–2μ diam.) atrobrunneorum levium, ramificantium et anastomosantium, cum ramulis numerosis, formans. Sporae atrobrunneae, globosae, dense sed inaequaliter spinulosae, 10–14 (–16)μ diam.

Sporangia gregarious, stalked, globose to broadly ovoid, 1–1.25 mm high, 350–450μ in diameter, many subtended by a brownish, membranous circular hypothallus; stalk ½–⅔ (–¾) of total height, externally dark orange or dark brown, glossy, faintly striate, consisting



FIGURES 1–2.—*Diachea silvaepluvialis* sp. nov.: 1, Habit, ×25; 2, portion of capillitium and 4 spores, ×900.

TABLE 2.—*Monthly distribution of myxomycete species collected and development periods for moist chamber cultures*

Species	Number of specimens collected			Development periods (days) for moist chamber specimens
	January	February	March	
Ceratiomyxales				
Ceratiomyxa fruticulosa	5	6	3	
C. sphaerosperma	1			
Liceales				
Cribraria intricata	1	1	1	
C. languescens	1	1		
C. microcarpa	2[a]	3[b]	1	10, 14, 23, 25, 25
C. minutissima	1[a]+1[b]			12, 24
C. tenella			3	
C. violacea	3[a]+2[b]	3[a]+3[b]		7, 10, 11, 12, 14, 14, 14, 15, 16, 23, 25
Dictydium cancellatum	3	6		
Licea operculata	2[a]	3[b]		11, 14, 20, 23, 28
Lycogala epidendrum	1	4	3	
L. exiguum	3	1	1	
Reticularia lycoperdon	3	1	1	
Tubifera ferruginosa			1	
T. microsperma			2	
Trichiales				
Arcyria cinerea	8+2[b]+1[c]	5+1[b]	1	12, 15, 24, 54
A. denudata	10	6	2	
A. incarnata	3		4	
Hemitrichia paragoga			1	
H. serpula	8	3	3	
H. stipitata	10	6	2	
H. vesparium	4+1[b]	2+1[b]	1	28, 51
Perichaena chrysosperma	1	1		
P. depressa	8	2	1	
P. minor			1	
P. vermicularis	1[b]	2[b]		23, 25, 34
Trichia favoginea	2	6	2	
Echinosteliales				
Echinostelium cribrarioides	1[a]			24
E. minutum	1[a]	2[b]		17, 20, 27
Stemonitales				
Clastoderma debaryanum	1	2		
Comatricha aequalis		2	2	
C. elegans	1[b]			24
C. irregularis	1		3	
C. longa	7		1	
C. subcaespitosa	1		3	
C. typhoides	5+1[b]		1	15
Diachea bulbillosa	1	1		
D. leucopodia			2	
D. silvaepluvialis	1		1	
Lamproderma arcyrionema	1+2[b]	1+2[b]	2	14, 43, 66, 77
L. scintillans	1	1	4	
Macbrideola martinii		1[b]		20
Stemonitis axifera	3	1	2	
S. smithii	2		1	
S. flavogenita	2 or 3			
S. fusca	6	3	2	
S. hyperoptera	2			
S. nigrescens			1	
S. splendens	3	3		
S. webberi	1	2	3 or 4	

See footnotes at end of table.

TABLE 2.—*Monthly distribution of myxomycete species collected and development periods for moist chamber cultures*—Continued

Species	Number of specimens collected			Development periods (days) for moist chamber specimens
	January	February	March	
Physarales				
Badhamia affinis			1 or 2	
Craterium aureum			1	
C. leucocephalum			3	
Diderma chondrioderma		1		
D. effusum	2	8+1[b]		44
D. hemisphaericum	1[b]	1	4	17
D. spumarioides	1			
Didymium clavus		1	2	
D. comatum			1	
D. crustaceum			1	
D. difforme			1	
D. intermedium			1	
D. iridis	2	1+1[b]		28
D. minus			1	
D. nigripes	3	7	3	
D. squamulosum		7	12	
Fuligo cinerea	1	1[a]		26
F. septica	1	9	3	
Physarella oblonga	2	4	1	
Physarum aeneum		1	4	
P. auriscalpium	1[b]	1+1[b]		15, 31
P. bogoriense	2	4	3	
P. bubalinum	1+?1[c]			ca. 29
P. cinereum			3	
P. compressum	7	8	2	
P. didermoides		4		
P. echinosporum			2	
P. galbeum		1		
P. lateritium			1	
P. leucocephalum		1[a]+2[b]		15, 20, 23
P. ?leucopus	1[c]			ca. 29
P. melleum	1[a]	2	12	67
P. notabile		1[a]		23
P. nucleatum	6	8	4	
P. nutans	2	2+1[a]	1	7
P. oblatum		1		
P. penetrale	1			
P. polycephalum	1	1	3	
P. psittacinum		2	2	
P. pulcherripes	1	1	1	
P. pusillum	1[a]	1+1[a]+1[b]		12, 43, 50
P. roseum			1	
P. ?rubiginosum	1			
P. stellatum	3	2		
P. tenerum	3	1		
P. viride	2+ 1[c]	4+1[b]		23, 36

[a] =m.ch., collected and harvested the same month.
[b] =m.ch., harvested the following month.
[c] =m.ch., collected in January, harvested in March.
Unmarked=field collections.

of a translucent, brown membrane densely packed with white, single or aggregated, more or less angular lime crystals 5–15μ in diameter; basally enlarged, apically continued through the entire sporangium as a more or less cylindrical columella. Peridium delicate, moderately silvery-iridescent, usually persisting at base of sporangium as a broad, slightly rugose disc or shallow cup, pale brown and smooth by transmitted light. Capillitium arising all along columella, consisting of an open, loose, easily detached network of delicate, dark brown, smooth, slightly wavy, branching and anastomosing threads 1–2μ in diameter, with many concolorous or slightly paler free ends. Spores dark brown in mass, dark purplish brown by transmitted light, globose, closely but unevenly spinulose, sometimes with a densely warted area 3.5–5.0μ in diameter, 10–12μ (*2197*) or 10–14(–16μ (*2998*) in diameter.

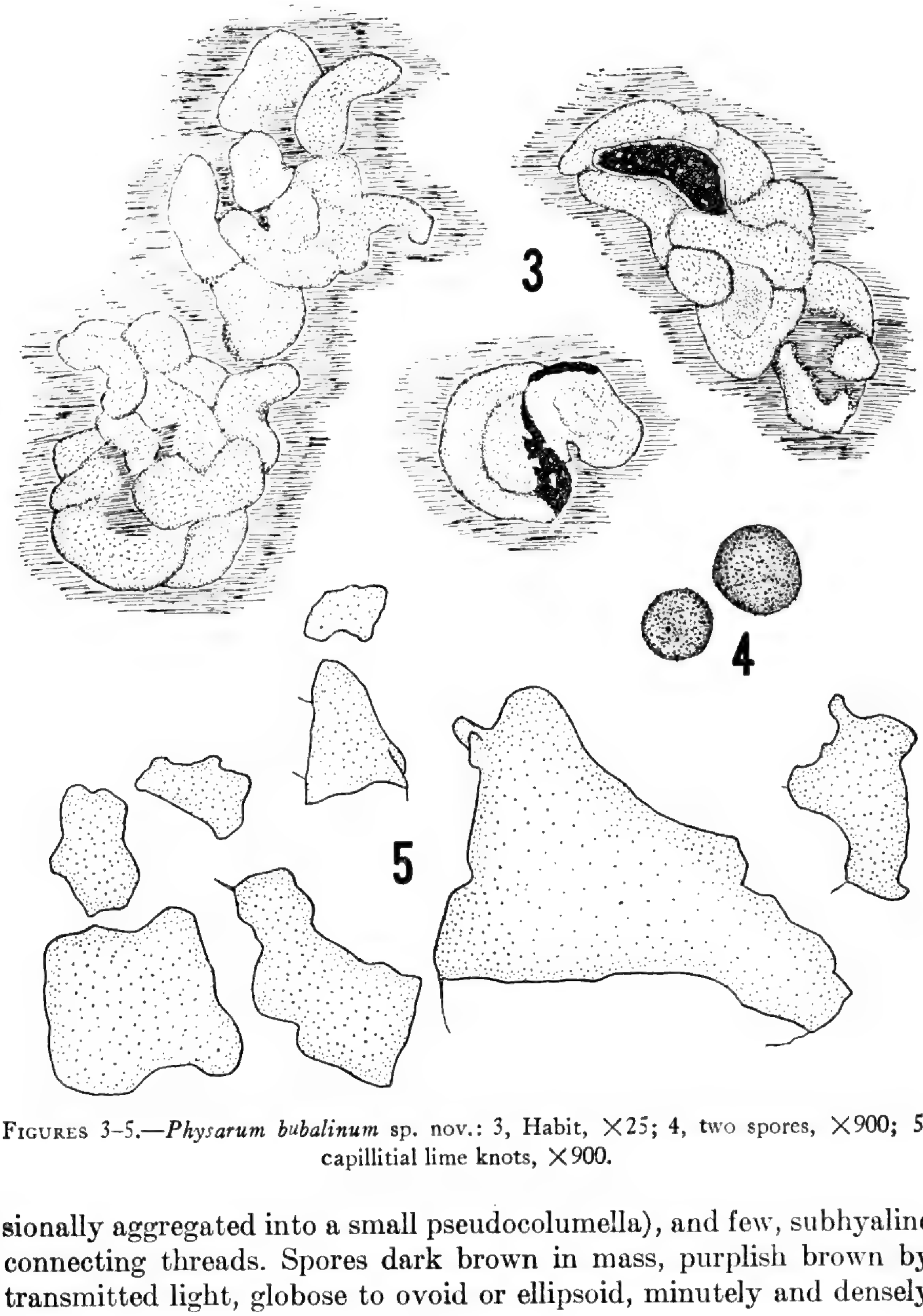
Holotype: B.W.I., DOMINICA: St. George parish, road from Laudat to Fresh Water Lake, elev. 2,200–2,500 ft. (**9**), on moist, decaying leaves on shaded ground, Farr *2197* (BPI). Paratype: St. Andrew parish, Central Forest Reserve, Borne area, elev. 1,400 ft. (**13**), on moist, dead leaf on shaded ground in rain forest, Farr *2998* (BPI).

Two species of *Diachea* with nonwhite stalks have been described. In *D. thomasii* Rex the lime itself is bright orange; the hypothallus is venulose and likewise orange; the sporangia are sessile or short-stipitate and larger, and the columellae much smaller than in *D. silvae-pluvialis*. *Diachea megalospora* Thind & Manocha evidently is very similar to *D. thomasii*, differing from the latter only in having slightly larger and more coarsely marked spores.

Physarum bubalinum, sp. nov. Figures 3-5

Sporangia fasciculos vel rosulas gregarias 1–3 mm diam. formantia, sessilia vel pseudostipitata, bubalina, plusminusve convoluta, leviter compressa, ca. 250μ lata, unitunicata; hypothallus nigellus, corneus, inconspicuus; peridium membranaceum, albidum, granulis calcareis bubalinis incrustatum; columella nulla; capillitium ex nodulis albis maximam partem grandibus, angularibus vel elongatis et filis paucis subhyalinis constans, aliquando pseudocolumellam formans; sporae atrobrunneae, globosae vel ovoideae vel ellipsoideae, minute et dense spinulosae, 10–12 vel 10$\times$12μ diam.

Sporangia in gregarious clusters or rosettes 1–3 mm in diameter, sessile or borne on black, weak, stalklike extensions of the hypothallus, convoluted to nearly pseudoaethalioid, buff, slightly compressed laterally, ca. 250μ thick. Hypothallus blackish, horny, inconspicuous. Peridium single, membranous, whitish, densely encrusted with tawny or pale brown, sometimes fading, clusters of lime granules. Columella none. Capillitium consisting of white lime nodes greatly varying in size and shape but predominantly large and angular or elongated (occa-



FIGURES 3–5.—*Physarum bubalinum* sp. nov.: 3, Habit, ×25; 4, two spores, ×900; 5, capillitial lime knots, ×900.

sionally aggregated into a small pseudocolumella), and few, subhyaline connecting threads. Spores dark brown in mass, purplish brown by transmitted light, globose to ovoid or ellipsoid, minutely and densely spinulose, 10–12 or 10×12μ in diameter.

Holotype: B.W.I., DOMINICA: ST. JOSEPH parish , along Layou River near Clarke Hall Estate, elev. ca. 200 ft. (1), on outside of rind of cacao fruit (*Theobroma cacao* L.) rotting in deep shade, Farr *2101* (BPI).

A scanty moist chamber development with broken but apparently similarly shaped, iridescent sporangial clusters and similar spores may represent a completely limeless phase of this species (collected

in St. Peter parish, summit of Morne Diablotins, elfin woodland, elev. 4,700 ft., on stem of *Lobelia stricta* Sw. in moist chamber, Farr *3033b*).

This myxomycete has similarities to several known species of *Physarum*, but cannot be accommodated in any of them. From *P. nicaraguense* and convoluted forms of *P. compressum* it differs mainly in its sessile habit and tawny color; from *P. gyrosum* in color, capillitial structure, and spore size. Two closely related, temperate-zone species, *P. virescens* and *P. confertum*, sometimes produce clumped, off-color sporangia resembling those of the new species in shape, but considerably smaller and with more delicate capillitium; *P. virescens*, furthermore, has smaller, smoother spores.

Annotated List of Species

The species of myxomycetes are listed in alphabetical order within the genera; these, in turn, are arranged alphabetically under the nowadays generally accepted orders Ceratiomyxales, Liceales, Trichiales, Echinosteliales, Stemonitales, and Physarales. The localities are cited according to parishes, starting with St. Joseph, and arranged in a clockwise direction. Within each parish, numbered localities, listed in ascending order (locality numbers printed in boldface), precede those without a number. For the unnumbered locations, only those elevations above 100 ft. are mentioned.

Order CERATIOMYXALES

Ceratiomyxa fruticulosa (Müll.) Macbr. No. Amer. Slime-Moulds, 18. 1899.

Distribution: Cosmopolitan.

St. Joseph: **1**, near underside of wet, decaying log, *2122*; **2** (Cocoa Centre), on underside of wet, rotting, decorticated log, *2552*, *2568;* ca. ⅓ mile S. of Mero, at mouth of Mero River, on rotting log, *2506*. St. Andrew: **5,** on underside of wet, rotten log, *2590*. St. David: **8,** on wet, rotting log, *2151*, *2289*, *2915*, *2916* (the latter poor); **15,** on rotten logs by river and in banana plantation, *2737* (scanty); 1.5 miles S. of Castle Bruce, on underside of very rotten, wet, shaded log in forest, *2171* (yellowish). St. George: **9,** on wet, rotting, shaded log, *2199* (scanty). St. Paul: **7,** in hollow of decaying, wet stump, *2708*; on side of wet, rotting log, *3009*.

Ceratiomyxa sphaerosperma Boed. Misc. Zool. Sumatr. 24: 1. 1927.

Distribution: Central America, Antilles, Indonesia.

St. David: Rosalie Agric. Exp. Sta., ca. 1 mile NE. of town, near intersection of road to St. Sauveur, on fibers of decaying coconut husks, *2139;* the colonies appear globose but are seen, under a dissecting microscope, to consist of branches borne on gelatinous, more or less dichotomously branched stalks.

Order LICEALES

Cribraria intricata Schrad. Nov. Gen. Pl., 7. 1797.

DISTRIBUTION: Cosmopolitan.

ST. PETER: **11,** on underside of very wet, rotten, shaded log, *2078a.* ST. ANDREW: **5,** on underside of wet, very rotten log, *2592* (moldy). ST. PAUL: **7,** on rotting twig buried in leaf litter, *2821;* sporangia yellow, with fairly abundant free ends in the net.

Cribraria languescens Rex, Proc. Acad. Phila. 1891: 394. 1891.

DISTRIBUTION: Probably cosmopolitan.

ST. JOSEPH: **2** (Cocoa Centre), on extremely rotten, wet, decorticated log, *2560.* ST. ANDREW: Ca. 1 mile W. of Porte-La-Fin, on decaying polypore on rotting log, *2352* (moldy).

Cribraria microcarpa (Schrad.) Pers. Syn. Fung., 190. 1801.

DISTRIBUTION: Probably cosmopolitan.

ST. JOSEPH: **1,** on bark of large tree (? *Inga*) behind "cabana" at Clarke Hall swimming area, in moist chamber, *2846* (a reddish, slightly atypical fruiting with spores 8–10μ in diameter and many "giant spores"); also from bark of ?leguminous tree in cacao plantation, in moist chamber, *2989a*, associated with *Perichaena vermicularis* (*2989b*); also on bark of *Mangifera indica* L. in moist chamber, *2990;* **2,** on bark of *Mangifera indica* in moist chamber, *2367;* on bark of rotten log, *2783* (sporangia dull orange); Macoucheri Est., ca. ⅓ mile inland from W. coast, on bark of indeterminate tree in moist chamber, *2365.*

Cribraria minutissima Schw. Trans. Amer. Philos. Soc. II, 4: 260. 1832.

DISTRIBUTION: USA, South America, Europe, Asia, Dominica.

ST. JOSEPH: **1,** on bark of *Cocos nucifera* L. in moist chamber, *2363* (sporangia golden yellow). ST. PATRICK: Felicite, from exposed log on beach in moist chamber, *2476a;* associated with *Arcyria cinerea* (*2476b*).

Cribraria tenella Schrad. Nov. Gen. Pl., 6. 1797.

DISTRIBUTION: Cosmopolitan.

ST. DAVID: Ca. 1–1.5 miles E. of north branch of Ravine Deux Dleaus, S. of Bois Diable Ridge, elev. ca. 1,100–1,200 ft., on wet, decaying, decorticate log at edge of open, partly cleared rain forest, *3030.* ST. PAUL: **7,** on rotting log in banana plantation, *2831, 2833,* the latter associated with *Arcyria cinerea;* free ends in net not numerous. Lister (17) describes Dominica material as having "scarcely the rudiments of a cup," mostly round nodes, and no "free rays."

Cribraria violacea Rex, Proc. Acad. Phila. 1891: 393. 1891.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **1,** on bark of indeterminate tree (? *Inga*) in moist chamber, *2332a,* associated with *Licea operculata* (*2332b*); on bark of

"Salamanda" (botanical name as yet undetermined) in moist chamber, *2593a* (abundant); on bark of *Artocarpus communis* Forst. in moist chamber, *2864, teste* G. W. Martin; **2,** on bark of *Mangifera indica* in moist chamber, *2368* (4 sporangia); Mero, on bark of *Lagenaria siceraria* (Mol.) Standl. in moist chamber, abundant, *2595, teste* G. W. Martin; associated with *Physarum nutans* (*2596*). ST. ANDREW: **14,** on bark of *Carica papaya* in moist chamber, *2478, teste* G. W. Martin (sporangia of last 2 harvests larger); on bark of *Terminalia catappa* in moist chamber, *2369*. ST. PATRICK: Felicite, from exposed log on beach in moist chamber, *2475*. ST. LUKE: Pointe Guignard, from wood of exposed log near beach, in moist chamber, *2860;* South Chiltern House, elev. ca. 1,200 ft., on bark of indeterminate large tree with light gray, splintery, easily detachable bark, in moist chamber, *2722b*, associated with *Physarum notabile* (*2722a*). ST. PAUL: N. of Mahaut, near Rodney's Rock, on bark of *Terminalia catappa* in moist chamber, *2855*.

Dictydium cancellatum (Batsch) Macbr. No. Amer. Slime-Moulds, 172. 1899.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **1,** on underside of rotting log, *2362, 2480* (both very moldy), *2674* (good); **2** (Cocoa Centre), on underside of wet, rotting log, *2551* (mostly moldy), *teste* G. W. Martin; **3,** on top of wet, rotting log, *2616, 2902* (a beautiful specimen); Macoucheri Est., ⅓ mile inland from W. coast, on bark of decaying, shaded log, *2061*. ST. DAVID: **8,** near underside of wet, rotting log, *2661*. ST. GEORGE: Along trail to Trafalgar Falls, elev. ca. 1,000 ft., on wet log in shade, collected by Mrs. Clifford Evans, *2326* (3 sporangia).

Licea operculata (Wing.) Martin, Mycologia 34: 702. 1942.

DISTRIBUTION: USA (New England and Midwest), Panama, Europe, Japan, Dominica.

ST. JOSEPH: **1,** on bark of indeterminate tree in moist chamber, *2766,* determined by G. W. Martin; on bark of *Inga* sp. in moist chamber, *2859b,* associated with *Physarum leucophaeum* (*2859a*); on bark of indeterminate tree (?*Inga*) in moist chamber, *2332b,* associated with *Cribraria violacea* (*2332a*) (placement of this specimen into moist chamber for ca. 1 week, in May 1966, in Beltsville, Md., yielded 2 additional sporangia). ST. ANDREW: **14,** on bark of *Pterocarpus officinalis* in moist chamber, *2370*. ST. PAUL: Beauclair Est., ca. 0.9 mile W. of Springfield Est., elev. ca. 1,000 ft., on bark of tall, acacia-like leguminous tree in moist chamber, *2854*. My identifications of this species are based on Dr. Martin's determination of *2766*.

Lycogala epidendrum (L.) Fr. Syst. Myc. 3: 80. 1829.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **1,** on top of shaded, moist, decorticate log, *2599;* **2,** on wood of rather dry, rotten log, *2226* (peridium black); **3,** on

top of shaded, wet, decorticate, rotten log, *2613*, *2669*, *2890*, *2891;* *2890* resembles *L. exiguum*, but the peridial warts are not chambered (perhaps a young stage of the latter species). St. John: **4,** on top of rotting log, *2977*. St. Paul: Beauclair Est., ca. 0.9 mile W. of Springfield Est., elev. ca. 1,000 ft., on top of smooth, decorticate, rotting log, *2562*.

Lycogala exiguum Morg. Journ. Cincinnati Soc. Nat. Hist. 15: 134. 1893.

Distribution: Cosmopolitan.

St. Joseph: **1,** on rotting log, *2029;* **2,** on bark at top of rotting log, *2784* (blackish). St. Andrew: Ca. 1 mile W. of Porte-La-Fin, on log, *2353*. St. Patrick: La Pleine (Plaisance Bay, ca. 1 mile N. of La Ronde River), on side of decorticate decaying log, *2307*. St. Paul: **7,** on side of moist, rotting log, *2697*. This species seems to be more common in Dominica than in Jamaica and some other islands, where *L. epidendrum* predominates.

Reticularia lycoperdon Bull. Hist. Champ. France, 95. 1791.

Distribution: Cosmopolitan.

St. Joseph: **1,** on exposed side near bottom of decaying log, *2033;* on bark of decaying logs, *2843*. St. Andrew: **14,** near underside of fairly exposed, rotten member of log pile in clearing, *2245;* and on same log, *2341*. St. George: Roseau Botanic Gardens, on side of rotting hardwood log, *2636* (small aethalium).

Tubifera ferruginosa (Batsch) Gmel. Syst. Nat. 2: 1472. 1791.

Distribution: Cosmopolitan.

St. John: Northern outskirts of Portsmouth, along road to Cabrits, on decaying coconut log, *2958*.

Tubifera microsperma (Berk. & Curt.) Martin, Mycologia 39: 461. 1947.

Distribution: Probably cosmopolitan.

St. Joseph: **3,** fairly abundant on rotten log, *2911*. St. Paul: **7,** on rotting logs in banana plantation, *2825* (somewhat moldy).

Order TRICHIALES

Arcyria cinerea (Bull.) Pers. Syn. Fung., 184. 1801.

Distribution: Cosmopolitan.

St. Joseph: **1,** on end of decaying, wet log, *2031* (very poor), *2303*. St. Peter: **11,** on underside of wet, rotting, shaded log, *2083* (digitate form). St. Andrew: **5,** on underside of rotting log, *2589* (digitate form) and *2591* (associated with *Trichia favoginea*); on burned wood inside of hollow stump, *2625* (*teste* G. W. Martin); **13,** on rotting debris in rain forest, *2996*. This specimen, although microscopically typical of the species, manifests an unusual color variation. The sporangia are black on the outside and olivaceous yellow or drab internally, with black or iridescent, olivaceous-yellow calyculi and

long, black stalks. The globose, pale yellow spores, 7–8μ in diameter, exhibit, under the 90× oil-immersion objective, a faint but regular reticulation of 12–14 meshes per hemisphere. This characteristic, not mentioned for the species in any of the standard monographs, was also found in several other, authentic collections of *A. cinerea* (including the digitate form) both from the tropics and from temperate regions. ST. DAVID: **8,** on underside of wet, decaying log, *2286* (digitate form); **16,** on underside of moist, shaded, rotting log, *2313* (digitate form). ST. PATRICK: Felicite, in moist chamber from exposed log on beach, *2476b;* in moist chamber from another log, *2984*. ST. MARK: Scotts Head, on bark of indeterminate tree along beach, in moist chamber, *2988;* slightly aberrant in the pale flesh color of the sporangia, and in the larger spores (8–10μ). ST. GEORGE: **9,** in rain forest in shade, from a moist chamber in which an orange plasmodium was placed, *2366b;* along trail to Trafalgar Falls, elev. ca. 1,000 ft., on underside of wet, decaying, mossy log in shade, *2329* (very poor and moldy). ST. PAUL: **6,** on underside of wet, rotting log, *2203;* **7,** *2702* (very poor); **10,** *2273* (poor), *2427*.

Arcyria denudata (L.) Wettst. Verh. Zool.-Bot. Ges. Wien 35: Abh. 535. 1886.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **1,** on underside of rotting log, *2359, 2361* (the latter weathered and moldy); on underside of very damp, rotting branch on ground, *2773;* **3,** on underside of wet, decorticate, very rotten log, *2610*. ST. PETER (bordering ST. JOHN): **12,** on underside of rotting logs, *2374;* a weathered, chocolate-colored specimen having capillitium sculptured with nearly complete rings and some reticulate fragments. ST. ANDREW: **5,** on underside of rotting log in banana plantation, *2619;* **13,** on wet, rotting stump in rain forest, *3000*, collected as immature, brown sporangia; **14,** on underside of rotting log covered by leaves, etc., *2246, 2247*. ST. DAVID: **6,** on rotting logs in banana plantation, *2726;* **8,** on underside of rotting log, *2158* (sparse) and near underside of wet, burned, decorticate, rotten log, *2656* (associated with *Hemitrichia stipitata*); on bark near underside of rotting log, *2473* (weathered); **16,** on log, *2311*. ST. GEORGE: **9,** on underside of wet, rotting log, *2194* (sparse). ST. PAUL: **7,** on underside of wet, rotting log, *2695;* 2 miles NE. of Springfield Est., in pasture, elev. 1,800 ft., on underside of moist, decaying log, *2337* (sparse).

Arcyria incarnata (Pers.) Pers. Obs. Mycol. 1: 58. 1796.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **1,** on underside of moist, decaying log, *2301, 2842,* a pale-violet gathering with persistent patches of peridium, but with microscopic structure normal for the species; same data, *2844,* a "typical" specimen; **3,** on decaying herbaceous stem on rotten log, *3018*. ST. JOHN: Along border between W. and E. Cabrits, elev. ca.

100 ft., on logs, *2965* (a weathered, brown, scanty, collection). St. Paul: **10,** near underside of decaying log, *2270* (an anomalous development characterized by capillitium 6–8μ in diameter and covered only with closely set rings, and by many "giant spores"); same data, *2275* (a bright-pink fruiting consisting of extremely long and elastic sporangia).

Hemitrichia paragoga Farr, Bull. Inst. Jamaica, Sci. Ser. No. 7: 34. 1957.

Distribution: Antilles (Jamaica and Dominica).

St. Paul: **7,** on underside of wet, rotting log, *2879*. Although in battered condition, this specimen can be recognized as almost certainly conspecific with the Jamaican type of the species, collected in the rain forest of the John Crow Mountains; the Dominica fruiting has larger spores (9–11μ instead of 8–9μ), less spiny capillitium, and shorter tapered free ends.

Hemitrichia serpula (Scop.) Rost. ex List. Monog. Mycetozoa, 179. 1894.

Distribution: Cosmopolitan.

St. Joseph: **1,** on bark of decaying log, *2120, 2125;* **2,** on underside of greatly decayed, decorticate log, *2229;* on decaying coconut log near road, *2489, 2490;* Macoucheri Est., ⅓ mile inland from W. coast, on decaying, shaded branch, *2060,* (1 annular plasmodiocarp). St. John: **4,** on side of mossy, shaded, rotting log, *2972,* associated with *H. stipitata* (*2971*). St. David: **8,** near underside of decaying log, *2156;* on roots of filmy fern on wet, decaying log, *2293;* on underside of rotten log, *2461;* **16,** on bark on underside of rotting log, *2309, 2312*. St. Paul: **7,** on dead leaves buried in litter pile, *2826;* on rotting twigs, roots, and banana debris, *2878*.

Hemitrichia stipitata (Mass.) Macbr. No. Amer. Slime-Moulds, 207. 1899.

Distribution: Cosmopolitan.

St. Joseph: **1,** on wet, decaying log, *2032* (scanty), *2121, 2123* (the latter *teste* G. W. Martin); on very wet, rotten wood, *2725* (sporangia collected in red droplet stage, mature after 2 days); **3,** on decaying coconut petiole on ground, *2609*. St. Peter: **11,** on wet, shaded, decaying log, *2077* (poor). St. John: **4,** on exposed underside of rotting log, *2971,* associated with *H. serpula* (*2972*). St. Andrew: **5,** on underside of moist, rotting log, *2623*. St. Andrew/St. David border: Pagua Bay, on burned, fairly dry, shaded, rotting log on black sand beach, *2241* (sparse). St. David: **6,** on underside of wet, rotten log, *2219;* **8,** on bark near underside of decaying log, *2287;* on wet, decaying stump, *3006* (approaching *H. clavata* by its vaselike sporangia and slightly roughened capillitium); on underside of decaying log in rain forest, *2419;* Rosalie Agric. Exp. Sta., ca. 1 mile NE. of Rosalie, at junction of road to St. Sauveur, on underside of wet, rotting log, *2137*. St. Patrick: Felicite, near mouth of Sarisari River, on protected side of burned, dry, decorticate log ca. 10 ft. from beach, *2305*. St. George: Along trail to Trafalgar Falls, elev.

ca. 1,000 ft., on underside of very moist, shaded, decaying log, *2328*. St. Paul: **7,** on underside of moist, very rotten log, *2701;* **10,** on very rotten, crumbling log in rain forest, *2433*, *teste* G. W. Martin.

Hemitrichia vesparium (Batsch) Macbr. No. Amer. Slime-Moulds, 203. 1899.

Distribution: Cosmopolitan.

St. Joseph: **2** (Cocoa Centre), on decaying ?coconut log, *2549;* **3,** on underside of rotting log, *2614*. St. Peter: **11,** on bark on underside of rotting log, *2081*, *2082*. St. John: **4,** on wood, mossy bark, and protruding from loose bark on side of rotting log, *2976*. St. Andrew: Pointe Baptiste, elev. ca. 100 ft., on wood, *2258*. St. Patrick: Felicite, near mouth of Sarisari River, on rotting, moist, decorticate log in shade of *Coccoloba* grove ca. 15 ft. from beach, *2306*, *teste* G. W. Martin; from exposed, rotting log near road, in moist chamber, *2633*. St. Luke: South Chiltern House, elev. ca. 1,200 ft., on bark of *Mangifera indica* in moist chamber, *2982* (good material).

Perichaena chrysosperma (Curr.) List. Mycetozoa, 196. 1894.

Distribution: Cosmopolitan.

St. Peter: **11,** on bark of rotten log, *2079;* with capillitium bearing long spines, and with spores 10–12μ in diameter, subglobose to ovoid, some thinner-walled on one side. St. Paul: Beauclair Est., ca. 0.9 mile W. of Springfield Est., elev. ca. 1,000 ft., on underside of wet, very rotten, decorticate log, *2567*.

Perichaena depressa Lib. Pl. Crypt., 378. 1837.

Distribution: Cosmopolitan.

St. Joseph: **3,** on side of moist, rotting log, *2611;* between bridge near mouth of Layou River and W. coast, on decaying coconut petioles on ground, *2501;* Macoucheri Est., ca. ⅓ mile inland from W. coast, on bark of shaded, decaying branch, *2059;* sporangia hoary, pale greenish gray, with deep-orange capillitium. St. Peter: **11,** on bark of rotten log, *2078*. St. John: **4,** on underside of log, *2385* (moldy), *2974*. St. Andrew: **14,** on inner bark and protruding from cracks in outer bark of rotting log, *2248*, *2339*, *2340*. St. David: **8,** on decaying rootlets of filmy fern on bark of decaying log, *2285;* **16,** on decorticate, decaying log, *2308*.

Perichaena minor (G. List.) Hagelst. Mycologia 35:130. 1943.

Distribution: North America, Great Britain, Japan, Dominica.

St. David: **8,** on rotting log, *2800*, sporangia stipitate to sessile; capillitium yellow.

Perichaena vermicularis (Schw.) Rost. Monog. Sluzowce (Mycetozoa), Append. 34. 1876.

Distribution: Cosmopolitan.

St. Joseph: **1,** on bark of ?leguminous tree in moist chamber, *2989b*, associated with *Cribraria microcarpa* (*2989a*); **2,** on bark of

indeterminate tree in moist chamber, *2486*, partly ruined in transit; on bark of ?*Tabebuia* sp. in moist chamber, *2853* (capillitium showing long spines).

Trichia favoginea (Batsch) Pers. Neues Mag. Bot. 1: 90. 1794.

Distribution: Probably cosmopolitan.

St. Joseph: **3,** on rotting debris on decaying log, *2892*. St. David: **8,** on decaying twig on ground, *2280;* on dead leaf on decaying log in rain forest, *2422* (battered); in hollow, rotten stump in freshly cut forest, *2474;* on dead banana leaf, *2654;* on decaying, mossy log, *2659a*; on decaying, small root, *2914;* **16,** on bark of shaded, rotting log, *2310*. St. Paul: **7,** on underside of rotting log, *2700;* **10,** on decaying log, *2431*. All specimens reveal elaters 5–6μ or 6–7μ in diameter, and spores covered with the high, sharp, complete reticulation peculiar to *T. favoginea sensu strictu*. The elaters of *2654* bear short spines, and those of *2422* have many bulbous free ends; those of the other collections are smooth, and have short-tapered apices.

Order ECHINOSTELIALES

Echinostelium cribrarioides Alexop. Amer. Midl. Nat. 66: 391. 1961.

Distribution: Greece, Dominica.

St. Joseph: **1,** on bark of "Salamanda" (botanical name as yet undetermined) in moist chamber, *2364*, *teste* C. J. Alexopoulos. The sporangia differ from those of the Greek type collection in being chocolate brown rather than cream-colored, in lacking a conspicuous basal collar, and in exhibiting a denser capillitium.

Echinostelium minutum deBy. *in* Rost. Monog. Sluzowce (Mycetozoa), 215. 1874.

Distribution: Probably cosmopolitan.

St. Joseph: **1,** on bark of indeterminate tree (?*Inga*) behind "cabana" at Clarke Hall swimming area, in moist chamber, *2857;* Macoucheri Est., ca. ⅓ mile inland from W. coast, on bark of *Mangifera indica* in moist chamber, *2331* (very sparse, pinkish). St. Andrew: **5,** on bark of *Dacryodes excelsa* in moist chamber, harvested in abundance, *2927* (nearly white). Both pink and white forms are known from Jamaica; no color is indicated for collections from Trinidad.

Order STEMONITALES

Clastoderma debaryanum Blytt, Bot. Zeit. 38: 343. 1880.

Distribution: Probably cosmopolitan.

St. Joseph: **1,** on underside of very damp, rotting log in shade, *2127b* (mostly moldy); **3,** on side of wet, rotten log, *2668*. St. David: **8,** on white mold on underside of very rotten, wet, decorticate log, *2421*.

Comatricha aequalis Pk. Ann. Rep. N.Y. State Mus. 31: 42. 1879.

DISTRIBUTION: North America, Europe, Antilles, Africa.

ST. ANDREW: "Hill," ca. 2 miles W. of Pagua Bay, in banana plantation, on wet twig in leaf litter, *2951*. ST. PAUL: **7,** on underside of moist, very rotten log and on polypore, *2698* (sporangia cocoa-colored, somewhat clavulate); on underside of wet, rotting log, *3007* (moldy); Harris Soltoun Est., ca. 1.5 miles W. of Pont Cassé, elev. ca. 1,400 ft., on wet, shaded, rotting stump near footpath in disturbed rain forest, *2657* (spores 8–10μ in diameter).

Comatricha elegans (Racib.) List. Guide Brit. Mycetozoa ed. 3, 31. 1909.

DISTRIBUTION: USA, Europe, Southern Asia, Japan, Antilles.

ST. PETER (near border of ST. JOHN): **12,** on bark of *Dacryodes excelsa* in moist chamber, *2632*.

Comatricha irregularis Rex, Proc. Acad. Phila. 1891: 393. 1891.

DISTRIBUTION: North and South America, Antilles, Malaya, Japan, Australia.

ST. JOSEPH: **2,** on top of rotting coconut log, *2785*. ST. JOHN: **4,** on side of rotting log and on old polypores, *2975;* near mouth of Picard River, Prince Rupert Bay, near exposed underside of rotting log, *2956*. ST. DAVID: **16,** on fairly dry, decaying log, *2315* (slightly aberrant).

Comatricha longa Pk. Ann. Rep. N.Y. State Mus. 43: 70. 1890.

DISTRIBUTION: Probably cosmopolitan.

ST. JOSEPH: **2,** on bark on underside of dry, decaying log, *2230, teste* G. W. Martin. ST. ANDREW: **14,** in swamp-woodland, pendent from old fruiting body of *Trametes corrugatus* (Pers.) Bres. (*2256*, det. J. A. Stevenson) growing on underside of large, very rotten, decorticate *Pterocarpus officinalis* log, *2244;* on same log, *2347*, det. G. W. Martin. These specimens correspond well with Lister's (17) description (quoted from the collector's letter) of early Dominica material as "on a root [,] hanging down like a goat's beard." ST. DAVID: **16,** on bark of decaying log and on adjacent green leaves, *2316*, *2317*. ST. PAUL: **10,** on log, *2278* (a large fruiting on a silvery hypothallus, ca. 2 inches in diameter, similar in color to *Stemonitis flavogenita*); 1.5 miles E. of Pont Cassé, in banana plantation, elev. ca. 1,900 ft., on rotting log, *2930*.

Comatricha subcaespitosa Pk. Ann. Rep. N.Y. State Mus. 43: 71. 1890.

DISTRIBUTION: North and South America, Europe, Dominica.

ST. DAVID: 8, on bark of rotten logs and on twigs and debris covering bark, *2290;* practically completely covering a 2×0.5 ft. area on underside of wet, rotting log, *2918;* ca. 0.5–1 mile E. of north branch of Ravine Deux Dleaux, S. of Bois Diable Ridge, elev. ca.

1,100–1,200 ft., on wet rotting log in open, partly cleared rain forest, *3028* (capillitium with brown thickenings; spores globose to ovoid, 8–10μ in diameter, finely warted). St. Paul: **7,** over entire underside of rotting log and on nearby fern roots, leaves, moss, etc., *3010* (mostly moldy).

Comatricha typhoides (Bull.) Rost. ex List. Monog. Mycetozoa, 120. 1894.

Distribution: Cosmopolitan.

St. Joseph: **1,** on end of decaying log and on adjacent dead leaf, *2302*; **3,** on very rotten, wet log, *3020*, long-stalked. St. Andrew: **14,** on underside of very rotten, decorticate, wet *Pterocarpus officinalis* log, *2242*, *2243*, associated with *Arcyria denudata*. St. David: **6,** on underside of wet, rotting log, *2207* (abundant but moldy); 1.5 miles S. of Castle Bruce, elev. ca. 400 ft., on underside of shaded, wet, decaying log in forest, *2172*. St. Patrick: Felicite, near mouth of Sarisari River, on bark of *Calophyllum* (probably *C. antillanum* Britton) along road, in moist chamber, *2484*.

Diachea bulbillosa (Berk. & Br.) List. Journ. Bot. 36: 165. 1898.

Distribution: North America, Panama, Antilles, Asia, Africa.

St. David: Ca. 1 mile N. of St. Sauveur, on underside of living *Pandanus* leaves near roadside, *2168;* sporangia globose, silvery-iridescent; spores 10–14μ in diameter. St. Paul: **10,** on underside of dead leaves in forest litter, *2432*.

Diachea leucopodia (Bull.) Rost. Monog. Sluzowce (Mycetozoa), 190. 1874.

Distribution: Cosmopolitan.

St. Joseph: **1,** on wet, dead leaves and twigs in roadside litter pile, *2881*, a fine, abundant collection; **3,** on dead leaves, *2899*, with spores atypically small (6–8μ in diameter).

Diachea silvaepluvialis Farr (see p. 409)

Lamproderma arcyrionema Rost. Monog. Sluzowce (Mycetozoa), 208. 1874.

Distribution: Cosmopolitan.

St. Joseph: **1,** on bark of *Juniperus* sp. in moist chamber, *2849*, a beautiful collection consisting of small sporangia (ca. 0.2–0.4 mm. in diameter); on bark of *Artocarpus communis* in moist chamber, *2863;* **3,** near underside of very rotten, wet, decorticate log, *2663;* Macoucheri Est., ca. ⅓ mile inland from W. coast, on bark of *Mangifera indica* in moist chamber, *2985* (scanty but good). St. David: **8,** on underside of wet, rotting log, *2802* (moldy); ca. 1 mile N. of St. Sauveur, elev. ca. 400 ft., on decaying leaf debris by rotting, roadside log, *2169* (sporangia were collected in white droplet stage and turned purple within 3–4 hrs). St. George: **9,** on bark of *Clusia plukenetii* Urb. in moist chamber, *2983a*, associated with 2 sporangia of *Physarum pusillum* (*2983b*). St. Paul: **7,** on dead leaf in litter pile, *2941*.

Lamproderma scintillans (Berk. & Br.) Morg. Journ. Cincinnati Soc. Nat. Hist. 16: 131. 1894.

DISTRIBUTION: Probably cosmopolitan.

ST. JOSEPH: **1,** in wet leaf litter along road, *2884;* **2,** in wet leaf litter along road, *2778,* associated with *Didymium crustaceum* (*2777*). ST. PAUL: **7,** on wet, rotting plant debris on ground, *2713,* associated with *Didymium squamulosum* (*2712*); on dead leaves in litter pile, *2822* and *2829,* the latter with gold-colored peridia; Brantridge Est., ¾ mile E. of Pont Cassé, elev. ca. 2,000 ft., on bark of decaying twig among roadside herbs, *2129* (poorly developed). In my collections as in those cited by Lister (17), the capillitium is not conspicuously paler near the columella.

Macbrideola martinii (Alexop. & Beneke) Alexop. Mycologia 59: 114. 1967.

DISTRIBUTION: Antilles (Jamaica, Dominica).

ST. JOSEPH: **1,** on bark of large, indeterminate tree (?*Inga*) behind "cabana" at Clarke Hall swimming area, in moist chamber, *2858, teste* C. J. Alexopoulos; the second find of this species, which was discovered in Jamaica.

Stemonitis axifera (Bull.) Macbr. No. Amer. Slime-Moulds, 120. 1899.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **1,** near underside of shaded, decorticate, moist, rotten log, *2948,* with sporangia 5 mm. tall, and spores 4–7μ in diameter; **3,** near underside of rotting log, *2895a,* associated with 1 sporangium of *Physarum psittacinum* (*2895b*) (sporangia pale-ferrugineous, 6 mm. tall, containing spores 5–6μ in diameter); ca. 1 mile N. of Clarke Hall, elev. ca. 250 ft., on fairly dry, exposed, rotten log, *2100.* ST. DAVID: **8,** on wood of rotting log, *2155;* **15,** on rotten logs by river and in banana plantation, *2735.* ST. PAUL: 2 miles NE. of Springfield Est., elev. ca. 1,800 ft., on underside of very rotten, moist log in pasture, *2338.* The sporangium and spore measurements of *2948* and *2895a* place these two collections on the border of *S. smithii.*

Stemonitis smithii Macbr. Bull. Nat. Hist. Univ. Iowa 2: 381. 1893.

DISTRIBUTION: Probably cosmopolitan.

ST. JOSEPH: **3,** on rotting log, *2893.* ST. PAUL: **10,** on wood of rotting log, *2271, 2272;* sporangia pale reddish brown, subclavulate, 3–4 mm. tall; spores 5–6μ diameter. The numerous forms intergrading with *S. axifera* suggest that *S. smithii* may well represent a depauperate condition or diminutive form of *S. axifera* rather than a distinct species, although the possibility of two extensively hybridizing species is not ruled out.

Stemonitis flavogenita Jahn, Verh. Bot. Ver. Brandenburg 45: 165. 1904.

DISTRIBUTION: Probably cosmopolitan.

ST. JOSEPH: **1,** near underside of rotting log, *2360.* (This identification is somewhat doubtful. The surface net is rather stout and lacks

free ends, but the meshes are too small for *S. splendens;* the capillitium is strongly webbed). St. Paul: **4,** on underside of decaying log, *2269*; sporangia very slender, clustered; **7,** on dead leaves in litter pile, *2944*.

Stemonitis fusca Roth, Mag. Bot. Römer & Usteri 1²: 26. 1787.

Distribution: Cosmopolitan.

St. Joseph: **2,** on bark and splinter on decaying log, *2227;* **3,** near underside of rotting log, *2672;* on rotting plant debris and on wood, *2898;* on dead leaf, *2900*, partly associated with *Physarum pulcherripes* (*2901*) (spore markings faint); on cut end of wet, decorticate, rotting log, *3019*. St. Andrew: Pointe Baptiste, elev. ca. 100 ft., on bark near underside of fairly exposed, damp, rotten log, *2257* (spores slightly smaller than usual); ca. 1 mile W. of Porte-La-Fin, abundant laterally on bark of rotting log, *2350*. St. David: **6**, near underside of rather wet, decaying log, *2133;* **15**, on rotten logs by river and in banana plantation, *2734;* **16**, on bark of decaying shaded log, *2314* (surface net weakly developed); on decorticate, rotting log, *2318*. The spore markings of nos. *2734* and *2898* approach those of *S. virginiensis* Rex.

Stemonitis herbatica Peck, Ann. Rep. N.Y. State Mus. 26: 75. 1874.

Reported by Lister (17).

Distribution: Probably cosmopolitan.

Stemonitis hyperoptera Meyl. Bull. Soc. Vaud. Sci. Nat. 52: 97. 1918.

Distribution: North and South America, Europe, Antilles, Japan.

St. David: 8, on wet, rotten, decorticate log, *2152*. St. Paul: **10,** on bark near underside of rotting log, *2277* (spores 4–5μ).

Stemonitis nigrescens Rex, Proc. Acad. Phila. 1891: 392. 1891.

Distribution: USA, South America, Wales, Antilles.

St. Joseph: **3,** on side of rotten log, *2667* (surface net large-meshed).

Stemonitis splendens Rost. Monog. Sluzowce (Mycetozoa), 195. 1874.

Distribution: Cosmopolitan.

St. Joseph: **1,** on underside of rotting log, *2482*, with meshes of surface net 8–40μ in diameter (average 20μ), but mostly less than 20μ. St. Peter (border of St. John): **12,** on underside of rotten logs, *2378*. St. David: Rosalie Agric. Exp. Sta., 1 mile NE. of Rosalie, near junction with road to St. Sauveur, on bark and wood of decaying branch, *2140;* on fairly exposed rotting log in shade, *2321*. No. *2140* consists of fuscous, stunted sporangia borne in groups of dense fascicles; however, the columellae are tortuous above, dissipating below the apex, and other microscopic characteristics likewise are typical for the species. No. *2321* is a poorly developed but interesting collection approaching *S. confluens* Cke. & Ell. St. George: **9**, on

underside of rotting log in citrus orchard, *2448;* Roseau Botanic Gardens, on top of decaying hardwood log, *2635*.

Stemonitis webberi Rex, Proc. Acad. Phila. 1891: 390. 1891.

DISTRIBUTION: Probably cosmopolitan.

ST. JOHN: **4,** laterally on bark of decaying log, *2970;* along border between W. and E. Cabrits, elev. ca. 100 ft., on side of rotting log, *2964*. ST. ANDREW: In banana plantation ca. 100 yards inland (W.) from Pagua Bay, on burned log, *2953*. ST. DAVID: **15,** on rotten logs, *2732, 2739;* Baut Sable Bay, S. of Ravine Soudé, on shaded end of fairly exposed rotting log at S. end of black sand strip, *2319*. St. PAUL: **7,** on side of exposed log at edge of banana plantation, *2942*.

Order PHYSARALES

Badhamia affinis Rost. Monog. Sluzowce (Mycetozoa), 143. 1874.

DISTRIBUTION: Cosmopolitan.

ST. JOHN: Along border between W. and E. Cabrits, elev. ca. 100 ft., on bark of decaying log, *2962;* the specimen fits the species in all characters except for the unusual length of the stalks (up to nearly 1.5 mm.).

Badhamia sp. (**B. ?affinis**)

ST. JOHN: **4,** on moss on rotting log, *2973*. The fruiting bodies of both *Badhamia* collections are more or less completely dehisced, so that their original shapes are not clearly evident. The capillitium of no. *2962* is typical, reticulate, and the spores are blackish in mass, smoky brown with many showing a pale dehiscence line by transmitted light, globose to ovoid or ellipsoid, densely spinulose, and mostly 14–16μ in diameter. No. *2973* fits the description of var. *orbiculata* (Rex) G. List. (19; 15), reported by Lister from Antigua and considered by Martin (20) a synonym of *B. affinis*, although it does not compare well with some authentic specimens of var. *orbiculata*. The fruiting bodies (usually only their basal halves remaining) are sessile, probably sporangiate and plasmodiocarpous, and apparently somewhat flattened, as indicated by the single layer of parallel white spikes constituting the capillitium of each; the spores are distinctly violaceous brown in mass, light brown by transmitted light, globose, spinulose, and 10–12μ in diameter, which is below the size range generally known for *B. affinis*. Both collections are white, without any red or brown tinges even near the sporangial bases; they differ conspicuously from each other in habit, capillitium, and spore characteristics and are probably not conspecific.

Badhamia nitens Berk. Trans. Linn. Soc. 21: 153. 1853.

Reported by Lister (17).

DISTRIBUTION: USA, Europe, Antilles, Asia, S. Africa.

Badhamia panicea (Fr.) Rost. *in* Fckl. Jahrb. Nassau Ver. Nat. 27–28: 71. 1873.

Reported by Lister (17).

DISTRIBUTION: North and South America, Europe, Dominica.

Craterium aureum (Schum.) Rost. Monog. Sluzowce (Mycetozoa), 124. 1874.

DISTRIBUTION: Cosmopolitan.

ST. DAVID: **8,** on dead leaf in wet leaf litter at edge of freshly cut rain forest, *2913;* sporangia yellow, subglobose to turbinate, with small but distinct, thickened basal cup.

Craterium leucocephalum (Pers.) Ditm. *in* Sturm, Deuts. Fl. Pilze 1: 21. 1813.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **3,** on dead leaf in litter pile, *3017*. ST. JOHN: Northern outskirts of Portsmouth, along road to Cabrits, on dead coconut leaflet in litter pile, *2957*. ST. PAUL: **7,** on dead banana leaf in litter pile, *2835*, *teste* G. W. Martin.

Diderma chondrioderma (dBy. & Rost.) G. List. *in* List. Monog. Mycetozoa ed. 3: 258. 1925.

DISTRIBUTION: USA (Western and Midwestern), Europe, Asia, Dominica.

ST. PAUL: **10,** on decaying log, *2428;* fructification subsessile, consisting of several sporangia and 1 elongated plasmodiocarp; capillitium mostly slender.

Diderma effusum (Schw.) Morg. Journ. Cincinnati Soc. Nat. Hist. 16: 155. 1894.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **1,** on dead coconut leaf sheath still attached to young plant, *2758;* **2,** in moss on deeply shaded, decaying log, *2228*. ST. LUKE: South Chiltern House, elev. ca. 1,200 ft., on bark of *Calophyllum* sp. in moist chamber, *2981*. ST. DAVID: **8,** on leaf, twig, and rotten log, *2160;* on bark of decaying twig, *2417;* on dead leaves, *2424;* on decaying banana sheath, *2466;* on living fern leaf and dead phanerogamic leaf, *2658;* and on decaying, mossy log, *2659b*, associated with *Trichia favoginea* (*2659a*); on living moss and small leaves on rotten log, *2747* (poor); no. *2160* consists of extensive, sheetlike, perforated plasmodiocarps. ST. PAUL: **7,** around base of living banana plant and on nearby rotting debris, *2696*.

Diderma hemisphaericum (Bull.) Hornem. Fl. Dan. 33: 13. 1829.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **1,** on decaying bamboo cane and on dead leaves in wet litter pile along road, *2880;* on dead leaf, *2950;* **2,** on dead leaf in wet litter pile near road, *2780*. ST. GEORGE: **9,** from moist chamber containing a ±orange plasmodium in leaf litter, *2366a*, associated with *Arcyria cinerea* (*2366b*). The identity of the plasmodium was not ascertainable; Martin (1949) reports white or nearly white plasmodia

for both the *Diderma* and the *Arcyria*. St. Paul: **7,** on rotting plant debris on ground, *2711;* on dead leaves in litter pile, *2827*.

Diderma rugosum (Rex) Macbr. N. Amer. Slime-Moulds, 105. 1899.

Reported by Lister (17).

Distribution: USA (Eastern and Midwestern), Europe, Antilles, Asia.

Diderma spumarioides (Fr.) Fr. Syst. Mycol. 3: 104. 1829.

Distribution: Cosmopolitan.

St. David: **8,** on living herbaceous leaves among debris on ground, *2284;* peridium areolate; spores unevenly warted, 9–11μ in diameter. These traits agree essentially with Lister's (17) description of Dominica material.

Didymium clavus (Alb. & Schw.) Rab. Deuts. Krypt. Fl. 1: 280. 1844.

Distribution: Cosmopolitan.

St. Andrew: "Hill," SW. of Pagua Bay, elev. ca. 700 ft., on underside of rotting log in banana plantation, *3004;* sporangia single and discoid, or fused in groups of 2–4, with stalks remaining distinct. St. David: **8,** on underside of wet, rotten log, *2546* (sporangia widely scattered). St. Paul: **7,** on bark of rotting log, *2832*.

Didymium comatum (List.) Nann.-Bremek. Proc. Nederl. Akad. Wetens. Ser. C, 69: 361. 1966.

Distribution: North America (Pa., Que.), Great Britain, Japan, Dominica.

St. Paul: **7,** on dead leaf in litter pile, *2830;* a well-developed collection consisting of sporangia and plasmodiocarps and exhibiting the characteristic elastic capillitium and spore markings described by Nannenga-Bremekamp.

Didymium crustaceum Fr. Syst. Mycol. 3: 124. 1829.

Distribution: North and South America, Europe, Antilles, Hawaii, Japan.

St. Joseph: **2,** in wet roadside litter pile, *2777*, associated with *Lamproderma scintillans* (*2778*). Spores dark brown, densely and prominently spinulose, 10–14μ in diameter; outer peridial crust almost completely disappeared, perhaps because of the wet environment; inner peridium loosely covered with yellowish lime crystals; columellae large, whitish or yellow, apparently formed by the strongly invaginated sporangial bases.

Didymium difforme (Pers.) Gray, Nat. Arr. British Pl. 1: 571. 1821.

Distribution: North and South America, Europe, Antilles, Japan.

St. Joseph: **3,** on leaf litter and rotting banana debris on ground, *2665b*, associated with *D. squamulosum* (*2665a*).

Didymium intermedium Schroet. *in* P. Henn. Hedwigia 35:209. 1896.

DISTRIBUTION: USA (Mo.), Central and South America, Antilles, Japan.

ST. ANDREW: **13,** on very wet, rotting log in rain forest, *2999;* sporangia white, fascicled; stalks straw-colored.

Didymium iridis (Ditm.) Fr. Syst. Mycol. 3:120. 1829.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **1,** on living and dead leaves and stems lying among decaying cacao fruit on ground, *2763* (see comments under *D. nigripes*); slightly E. of Coulibistri, on outer surface of cacao fruit and on large pebble inside, *2097* (a poorly developed fruiting with prominent, globose, whitish columellae). ST. PETER (border of ST. JOHN): **12,** on dead leaf buried in litter, *2373* (poor). ST. PAUL: **10,** on bark of *Cecropia peltata* L. in moist chamber, *2769;* fruited on bark, filter paper, and glass.

Didymium minus (List.) Morg. Journ. Cincinnati Soc. Nat. Hist. 16:145. 1894.

DISTRIBUTION: Cosmopolitan.

ST. DAVID: **8,** on living banana plant, *2801a* (sporangia stipitate to sessile).

Didymium nigripes (Lk.) Fr. Syst. Mycol. 3:119. 1829.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **1,** on living and dead leaves and stems among decaying cacao fruits on ground, *2761*. ST. ANDREW: **13,** on dead leaf in litter pile at edge of rain forest, *2997;* sporangia nearly limeless; spores very unevenly warted, as in *Fig. 102g* of Lister (19). ST. DAVID: **8,** on dead leaf sheath, *2154;* on living and decaying banana sheaths on ground, *2291b*, abundant; on dead moss and leaves, *2425* (poor); on dead leaf, *2471;* on underside of basidiocarp of *Hymenochaete* (*2532;* probably *H. berkeleyana* [Mont.] Cke., fide P. L. Lentz), *2541* (very poor); on living leaves of *Carludovica plumieri* Kth., *2653;* on living petiole of *Colocasia* sp., *2744;* on living banana plant, *2801b;* on rotting leaf litter, *2928* (spores 10μ in diameter). ST. GEORGE: **9,** on living leaves of small, shaded herb, *2198*. ST. PAUL: **7,** on dead leaf on ground, *2704*, on dead grass leaf in debris pile, *2707*. Nos. *2763* (*D. iridis*) and *2761* were growing together; they are similar in microscopic structure and macroscopically as well, except that the former specimen has pale stalks and white columellae; the latter collection exhibits dark columellae and stalks darker than those of *2763*, but sometimes becoming translucent in the upper portion. Dr. Martin, who examined and discussed (personal correspondence) *2763*, *2761*, and *2801b*, believes that these stalk variations may be governed by different maturation rates. He also found the spores of 2 adjacent sporangia of no. *2801b* to differ in color and size, those of 1 sporangium

being 8–9μ and dark, and those of the other, 10–11μ and much paler.

The relationship between *D. iridis* and *D. nigripes* is still controversial. Laboratory culture work tends to support the existence of 2 distinct species (C. J. Alexopoulos, G. W. Martin, personal communications), but field collections provide numerous connecting forms. These may represent another example of 2 strongly hybridizing species.

Didymium squamulosum (Alb. & Schw.) Fr. Symb. Gast. 19. 1818.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **1,** on wet, dead leaves piled by roadside, *2883, 2885, 2887, 2889;* **2** (Cocoa Centre), on wet, decaying coconut leaflet on ground, *2550* (sparse); on dead banana leaf, *2774;* on wet, dead leaves by roadside, *2775,* associated with *Physarum melleum* (*2776*), and *2779;* **3,** on leaf litter and rotting banana debris on ground, *2665a,* associated with *Didymium difforme* (*2665b*); on dead leaf, *2894.* ST. ANDREW: **5,** on rotting banana leaf on ground, *2617* (malformed). ST. DAVID: **8,** on decaying twig and dead banana leaf, *2651;* on rotting banana debris, *2796;* in rain forest leaf litter, *2932.* ST. PAUL: **7,** on rotting banana leaves on ground, *2705, 2706, 2712,* associated with *Lamproderma scintillans* (*2713*); on leaf litter, *2828;* in piles of decaying banana leaves, *2874.* This species occurs in two distinct phases. Nos. *2828, 2883, 2887–2889, 2550, 2775,* and *2932* are characterized by globose sporangia covered by a powdery lime coating, and globose or somewhat depressed columellae; the remaining specimens exhibit discoid sporangia with strongly rugose peridia, and flat white columellae. No. *2894* has globose sporangia, but with strongly rugulose peridial lime; the columellae are formed by the deeply umbilicate sporangium bases. This exceedingly variable species appears to be much more common on this island than in Jamaica.

Fuligo cinerea (Schw.) Morg. Journ. Cincinnati Soc. Nat. Hist. 19: 33. 1896.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: Slightly E. of Coulibistri, on rind and inside of decaying cacao fruit, *2096.* ST. GEORGE: Chapara Est. (near road junction), S. corner of parish, elev. ca. 1,550 ft., on rotting fruit of *Artocarpus* sp. (*A. ?communis*) on ground, in moist chamber, *2767;* the plasmodium turned from tan through pinkish to white before fruiting.

Fuligo septica (L.) G. H. Weber *in* Wiggers, Prim. Fl. Holsat., 112. 1780.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **2,** on decaying coconut logs, *2493–2496; 2493* with more or less cream-colored cortex, others with rust-colored cortex and yellow capillitial lime; **2** (Cocoa Centre), on side of rotting log, *2548,* brown and largely moldy. ST. JOHN: **4,** on top of rotting log, *2969;* aethalium salmon-colored with darker or yellow margin. ST. ANDREW: **5,** around thin herbaceous stems and roots hanging from underside

of rotten log, *2588* (reported from rootlets of higher plants also by Duss, 8); aethalia pale tan or orange. St. David: **8,** on roots and on very rotten wood and debris in open, hollow stump, *2655*, with bright yellow, thick, rugose but fragile cortex and abundant, somewhat elastic, yellow capillitium; on wet, rotting log in disturbed rain forest, in somewhat open spot near trail, *2804*, resembling *2655* and associated with *Physarum pulcherripes* (*2803*); on top of rotting log, *2933*; a large fructification (ca. 3.5×2.5 inches) with cortex salmon-colored above, yellow below. St. George: Roseau Botanic Gardens, on decaying hardwood log, *2634;* Chapara Est., S. corner of parish, near road junction, elev. ca. 1,550 ft., in banana plantation by creek, girdling decaying stem of *Bambusa vulgaris* Schrad. 3–5 inches above root crown, and on stem of woody vine, *2444;* a poorly developed, whitish specimen covered with a nectriaceous fungus. St. Paul: 1.5 miles E. of Pont Cassé, elev. ca. 1,800 ft., on top of rotten log in rain forest, *2111;* cortex hard, light brown. The brilliant yellow color and, especially, the more or less strongly elastic capillitium, of nos. *2655* and *2804*, bring to mind *Erionema aureum* Penz. Lister (17) reports 1 yellow aethalium of *F. septica*.

Physarella oblonga (Berk. & Curt.) Morg. Journ. Cincinnati Soc. Nat. Hist. 19: 7. 1896.

Distribution: Cosmopolitan.

St. Joseph: **1,** near underside of decaying coconut log among moss and living leaves, *2759* (possibly polyploid, since the sporangia are almost twice the normal size with correspondingly thick stipes; microscopic features are typical in size and appearance); **2** (Cocoa Centre), on underside of rotten logs, collected as yellow plasmodium, fruited 16 days later, *2765;* **3,** on underside of rotting log, *2615*. St. Peter: **11,** on underside of wet, rotten, shaded log, *2080*. St. David: 8, on underside of wet, rotting log, *2146*, *teste* G. W. Martin, *2512* (a freshly formed fruiting in excellent condition). St. Paul: **7,** on underside of wet, rotting logs, collected as yellow plasmodium, fruited in moist chamber, *2865* (a beautiful, abundant collection).

Physarum aeneum (List.) R. E. Fr. Ark. Bot. 1: 62. 1903.

Distribution: USA (Eastern and Midwestern), South America, Antilles, Hawaii, Asia.

St. David: 8, near base of living banana plant, *2416*; plasmodiocarps brown, with iridescent inner peridium; capillitium whitish. St. Paul: **7,** on dead leaves in litter pile, *2836*, *2877*, *2945*, *2946*.

Physarum auriscalpium Cke. Ann. Lyc. N.Y. 11: 384. 1877.

Distribution: USA, South America, Antilles.

St. Joseph: Macoucheri Est., ca. ⅓ mile inland from W. coast, on bark of *Mangifera indica* in moist chamber, *2483;* spores 11–14μ in diameter, densely spinulose. St. David: 8, on decaying banana

sheath, *2469*. St. Luke: Pointe Guignard, on wood from exposed log near beach, in moist chamber, *2861* (fruiting abundantly on wood, filter paper, and glass).

Physarum bogoriense Racib. Hedwigia 37: 52. Feb. 18, 1898.

Distribution: Probably cosmopolitan; pantropical.

St. David: **8,** on decaying twigs and leaf sheaths, *2283;* on decaying leaf, *2291a*, associated with *Didymium nigripes* (*2291b*); *2426* (with *Didymium nigripes* sporangia growing on some plasmodiocarps); on base of living banana plant, *2660;* on dead banana leaf, *2743;* on dead leaf in rain forest, *2794*. St. Paul: **7,** on dead banana leaf, *2709;* on dead leaf, *2820;* in pile of wet, dead leaves, *3011*. All collections appear typical for the species, but Lister (17) reports sporangial color variations from reddish brown to buff, bright yellow, or nearly white.

Physarum bubalinum Farr (see p. 412).

Physarum cinereum (Batsch) Pers. Neues Mag. Bot. 1: 89. 1794.

Distribution: Cosmopolitan.

St. Joseph: **2,** on living and dead leaves and stems buried in debris pile in cacao-banana plantation, *2786;* N. side of Brook Hill Est., behind Clarke Hall, on living *Paspalum conjugatum* Berg. leaves, collected by J. L. Cunningham *66–393–D*, det. M. L. Farr. St. David: **8,** on living banana plant, *2795*. St. Paul: **7,** in pile of decaying leaves, *2824*.

Physarum compressum Alb. & Schw. Consp. Fungi, 97. 1805.

Distribution: Cosmopolitan.

St. Joseph: **1,** inside decaying cacao fruit, *2030;* on and in decaying cacao fruits and on dead leaf, *2102; 2126* (sporangia liquid when collected, ripened in collecting basket); *2760;* the last 3 collections represent the convolute form. **2,** on dead leaf in debris pile, *2787;* **3,** on decaying leaf on rotten log, *2666;* on moss on moist, rotting log, *2671* (sporangia fused in fascicles of 2 or 3); slightly E. of Coulibistri, in and on moist, shaded, decayed cacao fruits and on dead leaf, collected C. and B. Evans and M. L. Farr, *2098*, *2099;* spores of the latter specimen, cultured in the laboratory by C. J. Alexopoulos, yielded clustered, sessile, contorted and lobed (sometimes partly immature) fructifications which, upon subculture by Charles Mims, produced a crop of individual sporangia typical for *P. compressum*. St. Andrew: **13,** on dead leaf in rain forest, *2993* (a depauperate voucher specimen). St. David: **8,** on decaying plant fibers, *2418;* on wet, dead leaf and twig, *2543* (convoluted form similar to *2126*); on dead banana leaf, *2748;* **6,** on stalk of decaying banana inflorescence, *2727;* **15,** on dead leaf and rotting twig, *2733* (both *2727* and *2733* contain more or less typical sporangia mixed with fascicled and

convoluted fruit bodies); ca. 1 mile N. of St. Sauveur, on decaying leaf debris by rotting roadside log, *2167*. St. Paul: **10,** on decaying plant debris, *2279* (considered by Dr. Martin as an "excellent example of the species"). An early collection of this species reported by Lister (17) consisted of "compressed simple or lobed sporangia on gray stalks."

Physarum didermoides (Pers.) Rost. Monog. Sluzowce (Mycetozoa), 97. 1874.

Distribution: Cosmopolitan.

St. David: **8,** on decaying filmy fern debris on rotting log, *2420;* on living filmy fern and associated leaf litter on rotting log, *2467*, *2468;* on tree fern roots and debris on wet, rotting log, *2662*.

Physarum echinosporum List. Journ. Bot. 37: 147. 1899.

Distribution: Antilles, Indonesia.

St. Joseph: **1,** on dead leaves in wet litter pile along road, *2882*, *2949*.

Physarum galbeum Wing. ex Macbr. No. Amer. Slime-Moulds, 53. 1899.

Distribution: North and South America, Europe, Antilles.

St. David: **8,** near underside of moist, very rotten log, *2652;* a good, fairly typical specimen with bright yellow, globose sporangia, floriform dehiscence, and capillitium containing numerous elongated and branching yellow lime knots. Two additional fruitings observed—a bright yellow one from St. David and one with orange stalks from St. Peter—were too dilapidated to retain.

Physarum lateritium (Berk. & Rav.) Morg. Journ. Cincinnati Soc. Nat. Hist. 19: 23. 1896.

Distribution: North and South America, Europe, Antilles, Asia, Hawaii.

St. Paul: **7,** on dead leaf in litter pile, *2947;* a rather battered fructification containing mostly sessile sporangia with limeless, iridescent peridia enclosing capillitium fading from bright orange to pale yellowish, and spores 9–10μ in diameter, finely warted, with clusters of more prominent warts.

Physarum leucophaeum Fr. Symb. Gast., 24. 1818.

Distribution: North and South America, Europe, Antilles, New Zealand.

St. Joseph: **1,** on bark of *Inga* sp. in moist chamber, *2859a*, associated with *Licea operculata* (*2859b*) (stalks dingy-yellowish). St. Mark: Summit of Scotts Head, elev. ca. 100 ft., on bark of *Tabebuia pallida* (Lindl.) Miers in moist chamber, *2862* (somewhat abnormal). St. Luke: South Chiltern House, elev. ca. 1,200 ft., on bark of *Mangifera indica* in moist chamber, *2723* (spores slightly atypical, 10–14μ, spinulose).

Physarum ?leucopus Lk. Ges. Nat. Freunde Berlin Mag. 3: 27. 1809.

DISTRIBUTION: Cosmopolitan.

ST. PETER: Summit of Morne Diablotins (end of 2d ridge), elev. ca. 4,700 ft., on stem of *Lobelia stricta* in moist chamber, *3033a;* fruited somewhat abnormally on glass, destroyed during transit. This species is known from the Blue Mountains and Port Royal Mountains in Jamaica and apparently prefers the more temperate environments. The Dominica record must be regarded as uncertain for the present.

Physarum melleum (Berk. & Br.) Mass. Monog. Myxogastres, 278. 1892.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **1,** on decaying twigs among rotting cacao fruits, *2762;* on dead leaves, *2886* (a depauperate fruiting partly associated with *Didymium iridis*); **2,** on dead leaves, *2776,* associated with *Didymium squamulosum* (*2775*); **3,** on dead leaf, *2896, teste* G. W. Martin (stalks tawny to dark yellow, peridia dark yellow); *2897,* (stalks white). ST. ANDREW: **13,** on dead leaf on rain forest floor, *2995.* ST. DAVID: **8,** on decaying, wet banana leaf after 4 days of continuous rain, *2509;* on decaying log, *2798* (resembling *3026*); among moss on side of rotting log, *2929;* near north branch of Ravine Deux Dleaus, S. of Bois Diable Ridge, elev. ca. 1,100–1,200 ft., on dead leaf in litter pile in banana plantation, *3026, 3027;* both with whitish, slightly turbinate sporangia and strongly developed, white columellae. ST. PATRICK: Laronde, on bark of indeterminate tree in moist chamber, *3034* (fruited on glass). ST. PAUL: **7,** on dead leaves in litter pile, *2837, teste* G. W. Martin (a specimen with well-developed columellae and, often, additional lime aggregations in the center of the sporangia); in piles of decaying banana litter, *2875, 2876.* This species displayed considerable variation in sporangial color and shape and in development of columella, as also noted by Lister (17) for Antiguan material.

Physarum notabile Macbr. No. Amer. Slime-Moulds ed. 2, 80. 1922.

DISTRIBUTION: North and South America, Europe, Antilles.

ST. LUKE: South Chiltern House, elev. ca. 1,200 ft., on bark of indeterminate tree in moist chamber, *2722a.*

Physarum nucleatum Rex, Proc. Acad. Phila. 1891: 389. 1891.

DISTRIBUTION: Pantropical; probably cosmopolitan.

ST. JOSEPH: **3,** near underside of wet, decorticate, rotten log, *2612; 2670;* on underside of wet rotting log and on adjacent living weeds, *3021,* very abundant. ST. PETER (bordering ST. JOHN): **12,** on underside of rotting logs, *2375, 2377;* on decaying small roots, *2376.* ST. ANDREW: **5,** *2587,* (a very moldy voucher specimen). ST. DAVID: **8,** on upper side of wet, decaying log, *2149;* on decaying twig, *2157;* on inner bark near top of decaying log, *2472;* on loose inner bark of decaying twig, *2544;* on rotting plant debris on decayed log, *2746;* on wet, rotting log, *2917, 2931.* ST. PAUL: **7,** on living leaf and adja-

cent debris and on part of rotting log, *2943;* **10,** on wood of decaying twig, *2274;* on decorticate, rotten log, *2429*, *2430*. This species occurred on the island in 2 forms: (a) typical delicate sporangia with globose, white pseudocolumellae which, however, readily fell out of the dehisced sporangia; (b) a robust (?polyploid) variant, represented by specimens *2149*, *2274*, *2376*, *2429*, *2430*, and *2746*. Although of the same structure and color as typical material, the robust fruitings were much larger, lacked pseudocolumellae, but exhibited an abundant capillitium with numerous, large, rounded, white lime nodes.

Physarum nutans Pers. Ann. Bot. Usteri 15:6. 1795.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: Mero, on bark of *Lagenaria siceraria* in moist chamber, *2596*, associated with *Cribraria violacea* (*2595*); spores 9–12μ in diameter. ST. DAVID: **8,** on underside of decaying log, *2423*, abundant but more or less moldy; after 4 days of continuous rain, *2511* (limeless); on bark of rotting log, *2799;* **6,** near underside of moist, decaying log, *2134*. ST. PAUL: **10,** on rotting twig, *2276* (battered).

Physarum oblatum Macbr. Bull. Nat. Hist. Univ. Iowa 2:384. 1893.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **2,** on decaying coconut log, *2491* (faded).

Physarum penetrale Rex, Proc. Acad. Phila. 1891:389. 1891.

DISTRIBUTION: North America, Europe, Antilles, Asia, Africa.

ST. DAVID: **6,** on rotting log, *2205;* sporangia subovoid, yellow, with very delicate, orange stalks.

Physarum polycephalum Schw. Schr. Natur. Ges. Leipzig 1:63. 1822.

DISTRIBUTION: Cosmopolitan.

ST. ANDREW: **5,** on underside of rotting log in roadside banana plantation, *2618;* Porte-La-Fin, on bark near underside of rotting log, *2349*, an abundant fruiting. ST. PAUL: **7,** on dead leaf on ground *2834;* on dead leaves, stems, etc. in litter pile, *2838*, *2839* (abundant). The capillitium of *2834* strongly suggests *P. rigidum* (G. List.) G. List. Nos. *2349*, *2834*, and *2839* consist of unfused sporangia and represent "var. *obrusseum* (Berk. & Curt.) List."; no. *2838*, as noted by Dr. Martin, contains fused as well as simple sporangia. Dr. Alexopoulos obtained typical *P. polycephalum* fruitings from laboratory cultures of *2349* (private communication). This evidence obviously refutes previous recognition by several investigators (including me) of the variety *obrusseum*.

Physarum psittacinum Ditm. *in* Sturm, Deuts. Fl. Pilze 1:125. 1817.

DISTRIBUTION: USA, Europe, Japan, Dominica.

ST. JOSEPH: **3,** near underside of rotting log, *2895b* (1 sporangium, associated with *Stemonitis axifera* [*2895a*]). ST. DAVID: **8,** on underside of decaying, moist log, *2147*, *2148;* on end of wet, rotting log in

somewhat open spot in rain forest, *2803*, associated with *Fuligo septica* (*2804*). The sporangia of *2147* are globose, rusty orange, sometimes limeless and iridescent near the base; the stalks are limeless, red or orange brown; the peridial lime scales are orange and the capillitial lime, orange to whitish; *2148* is a moldy specimen having yellowish inner capillitial lime nodes, dark brown stalks, and brownish-iridescent peridia with red lime scales. No. *2803* is a collection intermediate between *P. psittacinum* and *P. pulcherripes*. Dr. Martin favors the latter identification, but, after restudying the BPI specimen (which is more plentiful and in better condition than the IA duplicate), I am inclined to place it tentatively in *P. psittacinum* because of the red stipes which are not calcareous throughout, but often partly covered with a thin layer of lime, and because of the rather large, angular lime nodes of the capillitium. Columellae, furthermore, appear to be lacking, but this is true also of Dominica collections considered to be *P. pulcherripes*. The yellow lime of this specimen imparts an atypically pale aspect to the sporangia, but this may be due to fading.

Physarum pulcherripes Pk. Bull. Buffalo Soc. Nat. Sci. 1: 64. July 1873.

DISTRIBUTION: North America, Panama, Ireland, Dominica.

ST. JOSEPH: **3,** on decaying, decorticate log and dead leaf, *2901*, partly associated with *Stemonitis fusca* (*2900*); an abundant, well developed fruiting with yellow, calcareous stalks and deep golden- or rust-colored peridia. ST. DAVID: **6,** on rotting log, *2204*. ST. PAUL: **7,** on underside of wet, rotting log, collected as big, yellow, "knotty" plasmodium, *2772*. This species appears to be closely allied to *P. psittacinum*, differing from the latter (according to the standard monographs) by having calcareous stalks slightly prolonged inside the sporangial bases into short columellae, and small, rounded (rather than large, angular) capillitial nodes. Both species appear to be capable of considerable color variation, as judged from material examined. Since the spores of the 2 species are similar and since no columellae were found in any Dominica collections cited, stalk and capillitium traits were the diagnostic features most strongly relied on. A comparison with part of the type of *P. pulcherripes* revealed that the capillitia of the latter collection and of all Dominica gatherings are identical, but also that all contain numerous angular nodes of various sizes. The stalks of the type are strongly rugulose, bright orange, and calcareous in the upper half, but smoother, brown, and limeless in the lower; those of nos. *2772* and *2901* have strongly rugulose, yellow or whitish, calcareous portions, and slightly slimmer, smoother, brown, limeless sections; the latter may be apical, basal, or both. No. *2204*, a rather battered collection, has nearly limeless stalks. In all specimens the calcareous and noncalcareous sections of most stalks are sharply delimited.

Physarum pusillum (B. & C.) G. List. *in* Lister, Monog. Mycetozoa ed. 2, 64. 1911.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **1,** on bark of *Delonix regia* (Boj.) Raf. in front of Clarke Hall annex, in moist chamber, *2235;* on bark of *Juniperus* sp. next to Clarke Hall (main bldg.), in moist chamber, *2721* (capillitium scanty); *2771,* an improperly matured field collection. ST. GEORGE: **9,** on bark of *Clusia plukenetii* in moist chamber, *2983b,* associated with *Lamproderma arcyrionema* (*2983a*).

Physarum roseum Berk. & Br. Journ. Linn. Soc. 14: 84. 1873.

DISTRIBUTION: Florida, Brazil, Antilles, Africa, Asia, Oceanica.

ST. DAVID: 1–1.5 miles E. of north branch of Ravine Deux Dleaus, S. of Bois Diable Ridge, elev. 1,100–1,200 ft., among moss on side of rotting stump at edge of partly cleared rain forest, *3029* (a very poor, moldy, but distinctly recognizable specimen).

Physarum rubiginosum Fr. Symb. Gast., 21. 1817.

DISTRIBUTION: USA, Europe, Antilles.

ST. PETER: **11,** on bark of fallen branch, *2076;* a very small fructification consisting of short-stipitate sporangia and a small plasmodiocarp with deep orange lime scales on the peridium and white capillitial lime; tentatively identified by C. J. Alexopoulos and also by T. Brooks.

Physarum stellatum (Mass.) Martin, Mycologia 39: 461. 1947.

DISTRIBUTION: North and South America, Antilles, Africa, Asia; probably pantropical.

ST. PETER: **12,** on rotting log in rain forest, collected by G. Brooks, *2383* (moldy). ST. DAVID: **6,** on underside of decaying, wet log, *2206* (good, abundant material). ST. PAUL: **7,** on underside of mossy, rotten log, *2699* (with large pseudocolumellae); on decaying roots and other plant debris on ground, *2710;* **10,** on underside of moist, decaying log, *2268a* (a large fruiting).

Physarum tenerum Rex, Proc. Acad. Phila. 1890: 192. 1890.

DISTRIBUTION: Cosmopolitan.

ST. ANDREW: **14,** on rotting log in swamp-woodland, *2249,* collected as yellow plasmodium. ST. DAVID: **8,** on very rotten log, *2445;* collected as yellow "knotty" plasmodium, ripened overnight in moist chamber. ST. PAUL: **7,** on side of wet, rotting log, *2703;* stalks bright orange in *2445* and *2703*. Nos. *2249*, *2703*, (and *2170*, a depauperate collection from ST. DAVID, which was later discarded) are of doubtful affinity. Although these collections fit *P. tenerum* in every other respect, their stalks are limeless; *2703*, furthermore, has globose pseudocolumellae similar to those of *P. stellatum*, but yellow; *2249*, while lacking pseudocolumellae, shows enlarged or massive lime nodes in the center of the sporangia. The presence or absence of lime in the stalk has generally

been considered a reliable diagnostic character and is often used to separate species in this genus; a number of authentic collections examined (including the type) of *P. tenerum* all had calcareous stipes. Since, in general appearance, dehiscence, capillitium, and spores, the Dominica specimens are indistinguishable from typical members of this species, they are filed here until more is known about the significance and stability of lime content in the stalks.

Physarum viride (Bull.) Pers. Ann. Bot. Usteri 15: 6. 1795.

DISTRIBUTION: Cosmopolitan.

ST. JOSEPH: **2** (Cocoa Centre), near underside of rotting log, *2598*, *teste* G. W. Martin (sporangia deep yellow). ST. PETER (bordering ST. JOHN): **12,** on bark of *Dacryodes excelsa* in moist chamber, *2845*. ST. ANDREW: **5,** on bark of *Dacryodes excelsa* in moist chamber, *2856* (largely moldy). ST. DAVID: **8,** on bark near underside of wet, rotting log, *2159* (a beautiful, deep orange fructification with concolorous stalks); *2161*, collected as yellow plasmodium, which produced, by the next day, ripe, globose, nodding, yellow-orange sporangia with small, limeless basal discs and orange stalks; *2542* and *2545*, with same coloration as *2161*, collected in slightly immature state. ST. GEORGE: **9,** in moist chamber from plasmodium in rotten wood, *2764a*.

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